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The Mammalian Fauna on the Islands at the Northern Tip of Sabah, Borneo

Shukor Md. Nor

Abstract

There are 39, 28, 15, and 11 species of mammals known from Banggi, Balambangan, Malawali, and Molleangen islands, respectively. More than 35% of the species on each island are reported here for the first time: 20 from Banggi Island, 10 from Balambangan Island, 6 from Malawali Island, and all 11 from Molleangen Island. Most of the new records on these four islands are bats of 21 species, including a very poorly known insectivorous species (*Pipistrellus vordermanni*). Others include two primates (*Tarsius bancanus* and *Nycticebus coucang*) and three civets (*Viverra tangalunga, Paradoxurus hermaphroditus,* and *Arctogalidia trivirgata*). Four insectivorous bats and a Bornean endemic tree squirrel (*Exilisciurus exilis*) were reported earlier either on Banggi or on Balambangan Island but were not found in this survey, presumably because they occur at very low density. Two species of rats (*Rattus tiomanicus* and *Sundamys muelleri*), two fruit bats (*Cynopterus brachyotis* and *Rousettus amplexicaudatus*), one ungulate (*Sus barbatus*), and a primate (*Macaca fascicularis*) are the most abundant mammalian species on these four islands. There are no conspicuous morphological differences among island populations, or between them and the adjacent mainland population, except for *Sundamys muelleri,* from Malawali Island; mean body size in this population is substantially smaller than in other populations. No endemic species are present on these islands, but three species otherwise restricted to Borneo are present on Banggi Island: *Tupaia gracilis, Exilisciurus exilis,* and *Hipposideros dyacorum.* In general, the mammalian fauna is shared among the islands and mainland Borneo and exhibits a characteristic feature of land-bridge island faunas: it follows a nested subset pattern that was shaped through selective extinction following the rise in sea level that began about 16,000 years ago. The −120 m bathymetric line is a boundary line that divides the Bornean fauna of these islands from the Palawan fauna of the Philippine Islands immediately to the north.

Introduction

The great tropical island of Borneo supports one of the richest mammal faunas on Earth; approximately 221 native species have been recorded there. Of these, 92 species are bats (Chiroptera) and 129 species are nonvolant. Nonvolant mammals are represented by 8 species of Insectivora, 10 species of Scandentia, 13 species of Primates, 56 species of Rodentia, 26 species of Carnivora, 12 species of Artiodactyla, and 1 species each of Dermoptera, Pholidota, Proboscidea, and Perissodactyla (Payne et al., 1985). Between 28 and 31 species of mammals are considered to be endemic to Borneo (Davis & Payne, 1982; Payne et al., 1985; Heaney, 1985b, 1986).

Of the 221 species of native mammals on Borneo, at least 160 have been found in Sabah. Of these, 52 species are bats. Among the nonvolant species, 19 are found mainly or only in upland regions and 89 are found mainly or only in the lowlands and low hills; 3 species have been found only on Mt. Kinabalu (Davis & Payne, 1982). Among 29 mammalian families in Sabah, the squirrels (Sciuridae) are the most diverse, with 15 genera and 27 species. Sabah's mammals include a number of exceptional species: the world's largest tree squirrel (*Ratufa affinis*), the smallest tree

squirrel (*Exilisciurus exilis*), the world's largest bats (*Pteropus vampyrus*), and the largest member of the Insectivora (*Echinosorex gymnurus*).

Although the checklist of mammals that occur on mainland Sabah is now considered to be virtually complete (Banks, 1949; Davis, 1962; Medway, 1977; Davis & Payne, 1982; Payne et al., 1985; but see also Emmons, 1993), little information has been gathered on the ecology and distribution of mammals from offshore islands. There are more than 20 islands off the north, west, and east coasts of Sabah, but only about 7 of them (Labuan, Tiga, and Gaya islands on the west coast and Banggi, Balambangan, Malawali, and Mengalum islands at the northern tip) have been surveyed, none intensively (Chasen & Kloss, 1931; Wells & Lowry, 1975; Medway, 1977; Wells, 1977; Omar et al., 1984; Payne et al., 1985).

Small nonvolant mammals previously known on these seven offshore islands represent six families (Muridae, Sciuridae, Tupaiidae, Soricidae, Cynocephalidae, and Erinaceidae), and large mammals represent four families (Cercopithecidae, Suidae, Tragulidae, and Cervidae). Among small mammals, murid rodents are the most diverse and occur on all islands; at the opposite extreme, the erinaceids are represented by a single species found only on Labuan. The two most widespread and abundant large mammal species found on most of the offshore islands are wild pig (*Sus barbatus*) and long-tailed macaque (*Macaca fascicularis*). Two other wild ungulates, deer (*Cervus unicolor*) and mouse deer (*Tragulus napu*), are known only from the largest of the offshore islands, Banggi and Balambangan.

Out of eight families of bats found on Borneo (Payne et al., 1985), six have been recorded from offshore islands of Sabah. Prior to this study, common bats (Vespertilionidae) were represented by seven species, followed by fruit bats (Pteropodidae) with five species, horseshoe bats (Rhinolophidae) with four, sheath-tailed bats (Emballonuridae) with two, and free-tailed bats (Molossidae) with one species (Chasen & Kloss, 1931; Medway, 1977; Omar et al., 1984; Payne et al., 1985). Bats are considered the most diverse mammals in Borneo, but they generally are poorly known. This is probably because many are small, agile, and difficult to catch, requiring special trapping methods (Payne et al., 1985).

Unfortunately, habitat destruction on the offshore islands of Sabah is proceeding very rapidly, due to both selective logging of primary forest and total clearing for agriculture. Because these islands have not been thoroughly sampled and little or no attention was given to them by previous collectors, little faunal information is currently available. Thus, the need to gather information while large areas of primary forest are still intact is of crucial importance.

The purpose of my study was twofold: to document the number of mammals occurring on Banggi, Balambangan, Malawali, and Molleangen islands at the northern tip of Sabah, and to obtain information on their basic ecology. The first three of these islands were surveyed in 1927 by a party from the Raffles Museum of Singapore (Chasen & Kloss, 1931) and later by Wells (1977) and Payne et al. (1985), and the systematics of the mammals was summarized by Medway (1977) and Payne et al. (1985). However, it seemed likely that the surveys were incomplete, and ecological information from these three islands and adjacent islands was almost entirely lacking.

This monograph reports the results of my survey of the mammals on four offshore islands of Sabah. All known previous records of mammals are included in this report (Chasen & Kloss, 1931; Wells, 1977; Payne et al., 1985). Because many mammals recorded in this survey had not been reported previously and the general ecology of species had not been documented, I present data on reproduction, description of habitats where animals were taken, and external and cranial measurements whenever possible.

Geology and Climate

Borneo is the fourth largest island of the world, covering an area of 743,244 km^2. The state of Sabah, at the northern tip of Borneo, occupies 76,115 km^2 and is flanked by many offshore islands, from the Brunei Bay on the east coast, across the Strait of Balabac at the north, and ending at Sibuko Bay on the west coast (Fig. 1).

The four study islands, Banggi, Balambangan, Malawali, and Molleangen islands, at the northern tip of Sabah (Figs. 1 and 2), are geologically similar in their formation, consisting of relatively young sediment. Their strata have been dated up to Upper Cretaceous/Eocene (Wilson, 1961).

Banggi Island

Banggi Island is the largest island along the coast of Sabah, with an area of 450 km^2. It is located about 20 km north of mainland Sabah, between

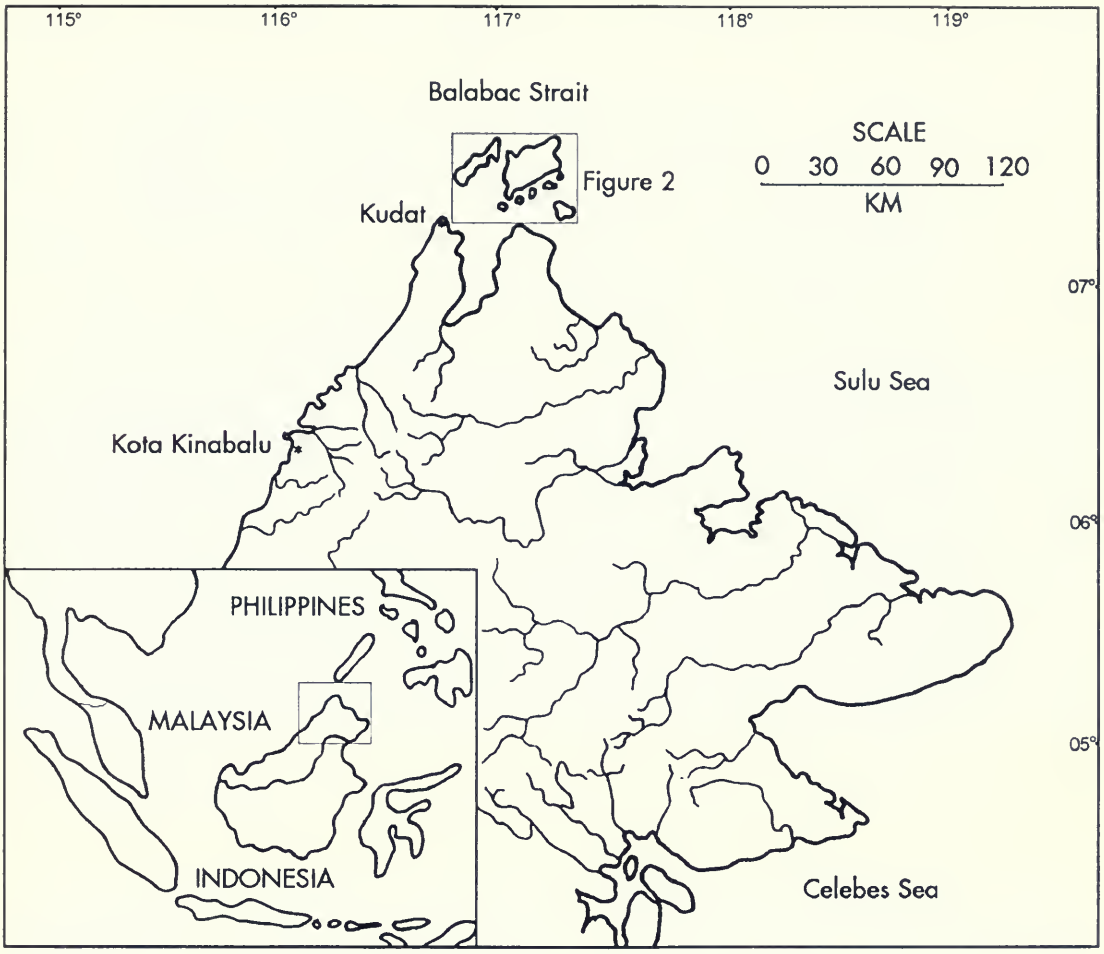

FIG. 1. Map of Southeast Asia and the northern part of Borneo.

longitude 117°3′ and 117°25′E and latitude 7°07′ and 7°23′N. The island is roughly oval in shape, about 29 km long and 20 km wide. The highest peak, Bukit Senambung, at 572 m, is near the northwest coast. Topographically, areas extending northeastward and southward from Banggi Peak (Bukit Senambung) are slightly hilly, decrease in elevation toward the center of the island, and are still lower farther south and west (Figs. 3 and 4).

The south and east coasts of the island are fringed with mangrove forest for most of their length. However, on the north and west coasts there are many sandy beaches, with only a few patches of mangrove forest developed at the mouths of rivers. There are few freshwater streams on the island; most are in the north and east, are short, run rapidly from their source over coarse boulder beds to the sea, and are potentially dry within a few weeks of cessation of rains, usually between May and June. On the east and south are saltwater streams, long and meandering across estuarine swamps.

Several small islands surround Banggi, mostly to the east and south, namely Patananum, Pagasan, Balak, Panukaran, Bilangan, Sibogok, Latuan, and Kagayan (Fig. 2). These islands are very low in elevation, and most are covered by mangrove forest (unpublished vegetational map based on 1972 forest inventory by Sabah Forestry Department).

Balambangan Island

This island, with an area of 150 km^2, lies between longitude 116°45′ and 117°2′E and latitude 6°10′ and 7°25′N, about 5 km west of Banggi Island and 30 km north of the mainland town of Kudat.

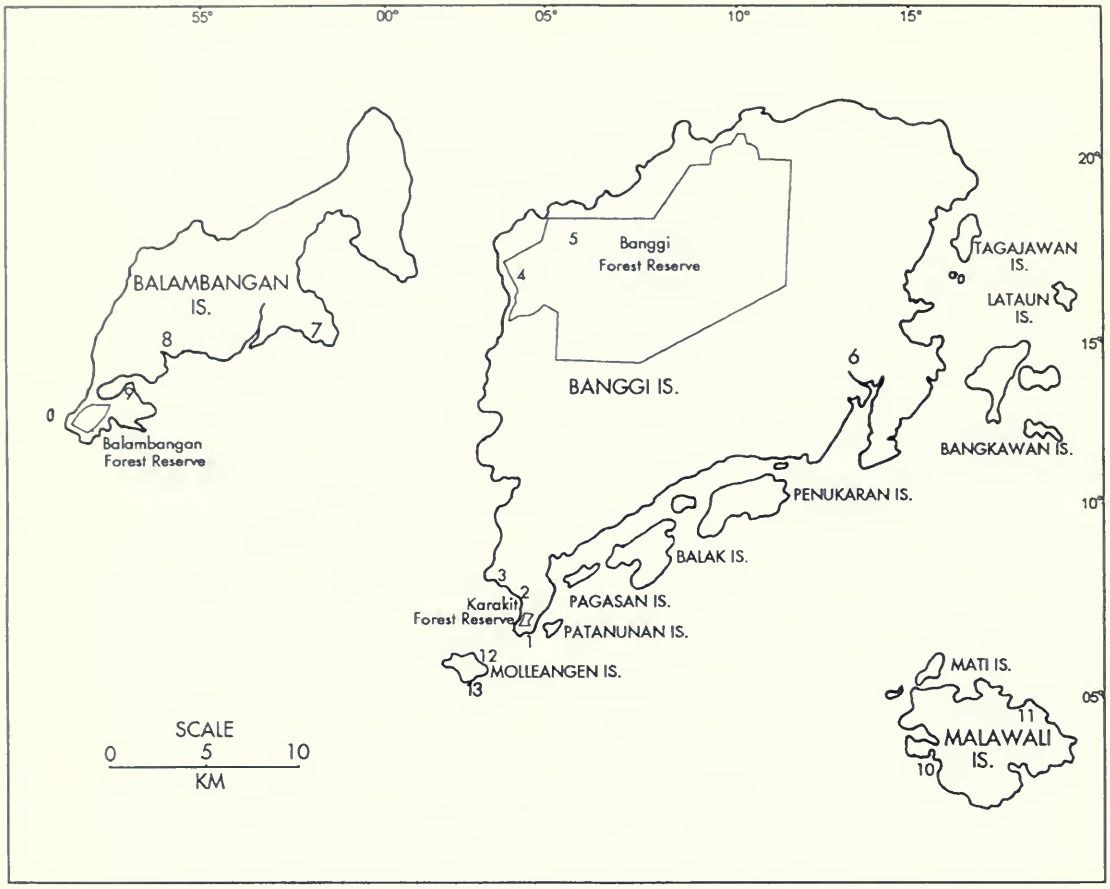

FIG. 2. Map of Banggi, Balambangan, Malawali, and Molleangen islands, showing major localities, forest reserves, and other adjacent islands, as mentioned in the text. Localities are indicated by number: 1, Karakit (Site A4); 2, Wak-wak (Site A1); 3, Lok Tohok (Site A5); 4, Kalangkaman (Site A2); 5, Banggi Peak; 6, Sabor (Site A3); 7, Tanjung Periok; 8, Selamat Darat (Site B1); 9, Kuak Simpol (Site B2); 10, Paramuan (Site C1); 11, Site C2; 12, Site D1; and 13, Site D2.

It is elongated in a northeasterly direction, is 20 km long, and has an irregular, deeply embayed southeastern coastline. The island is topographically homogeneous at its north and east, with the elevation increasing from its center toward the south. In the south, near Air Simpul (Kuak Simpul), the greatest elevation is reached on a 134-m peak (Figs. 2 and 5). This peak is flanked by prominent limestone cliffs, with a vertical cliff facing southeast toward Tanjung Kalutan. Most freshwater streams run from this hill, and most of them run to the south and the east of the island; they are very short and flow directly to the sea.

Malawali Island

Malawali Island has an area of about 45 km². It is oval in shape, about 8 km across from east to west, and about 5 km deep. Of the four islands in this study, it is the nearest to the mainland (15 km). It lies at latitude 7°04′N and longitude 117°10′E. The shore rises fairly rapidly from the sea, and the coastline is covered mostly by mangrove (Fig. 6). There are two beaches, at Paramuan on the west coast and at Malantak on the southeast coast. The interior is hilly; the highest peak, on the south coast, is 160 m (Fig. 2).

Molleangen Island

Molleangen Island (117°02′E and 7°05′N) lies at the southern tip of Banggi Island and covers an area of about 1.5 km². It is about 3 km from Tanjung Kammaung (on Banggi Island) and 15 km from the mainland. Three-quarters of this island is flat, and only a small portion at the southeast

FIG. 3. View of Banggi Peak (Bukit Senambung) from the west of Banggi Island. At the base of the peak is the trapping Site A2 (Kalangkaman).

is slightly elevated, with the highest peak at 120 m (Figs. 2 and 7).

Like other islands on the Sunda Shelf, these four islands previously were joined to the mainland and became isolated by rising sea level during the late Pleistocene. Based on the present depth of the sea between the islands and the mainland, I estimate that they were separated from the mainland about 9,000 years ago. This estimation is based on data from Dunn and Dunn (1977) and Fairbanks (1989), who hypothesized that a rapid rise in sea level, from −120 m, occurred beginning about 18,000 BP, to a level within 10 to 15 m of present sea level by 6,000 BP; the current sea level was established in about 2,000 BP (Fairbanks, 1989, Fig. 2).

Balambangan, Banggi, Malawali, and Molleangen islands lie on a bank less than 35 m deep. Balambangan Island is separated from Tanjung Sempang Mengayau, on the mainland, by a narrow channel 35 m deep. However, the channel is very shallow between this island and Banggi Island, being less than 10 m deep at the northern part. Between Banggi Island and the mainland is a short, narrow basin, running east and west, with a minimum depth of 35 m, varying between 80 m in the west and 50 m in the east. Malawali Island is nearest to the mainland, separated by a shallow watercourse 18 m deep. Much deeper water (ca. 145 m) separates these islands from the Balabac Islands to the north (U.S. Defense Mapping Agency, scale 1:200,000) (Fig. 2).

The climate of the four islands is considered equable. It is controlled by the monsoons; the wetter period occurs during the northeast monsoon, from October to February, and the drier season during the southwest monsoon, from March to September. Between monsoons there are periods of variable winds lasting about 6 weeks. During the dry season the islands receive an average rainfall of 100 to 150 mm. During this period, the northern part of the islands may not receive rain for several weeks, and many of smaller streams dry up. However, during the wettest season, rainfall may exceed 400 mm per month. The mean annual rainfall over 9 years (1982–1990) for Kudat District was 2,105 mm (unpublished data from Malaysian Meteorological Service, 1990). The dai-

FIG. 4. View from the top of Banggi Peak at 572 m. On the background, facing to north of the Banggi Island, is the forest, which was selectively logged probably as early as the 1960s.

ly maximum and minimum temperatures rarely exceed 32°C and 20°C, respectively. The atmosphere is always damp, with the relative humidity typically above 80%.

General Ecological Background

Reports on the flora of Banggi, Balambangan, and Malawali islands are those of Omar et al. (1984), Wells (1977), and Merrill (1924, 1926). Omar et al. (1984) also briefly described the habitats and the fauna of a few offshore islands of Sabah. Wells (1977) described habitats on Balambangan Island in a proposal to declare Balambangan Island a national park. Complete vegetational accounts of Banggi and Balambangan islands were compiled by Merrill (1924, 1926). My description of the habitats on these four islands was based on these references, plus records from the Sabah Forestry Department at Kudat, a vegetational map based on a forest inventory made in 1972, and general observations and botanical sampling during my survey.

Banggi Island

Most of the southeast coast is covered with mangrove forest, with *Rhizophora mucronata* as a dominant species. Areas further inland, toward the north and east, are covered with primary to lowland forest comprised of *Eugenia* sp., *Gluta* sp., *Calophyllum* sp., *Mangifera caesaria, Dimocarpus lingan, Adinandra* sp., *Durio grandiflorus,* and *Shorea* spp. (Omar et al., 1984). Most of the primary lowland forest is found within two forest reserves that were gazetted by the Sabah State Government in the early 1960s. The first forest reserve is the Banggi Forest Reserve (Commercial Forest Reserve Class II), located in the northeast portion of the island; it covers an area of about 11,206 ha. The smaller reserve is the Karakit Forest Reserve (Protected Forest Reserve Class VI) at the southern tip of the island, covering an area of about 24 ha. One mangrove forest reserve (Forest Reserve Class V) also was set aside at the southeast corner of the island, covering an area of about 11,504 ha (unpublished vegetational map based on 1972 forest inventory by Sabah Forestry De-

FIG. 5. View of trapping Site B2 (Kuak Simpol) from the southeast of Balambangan Island. On the background is the highest peak on Balambangan Island, at 134 m, flanked by prominent limestone cliffs with large vertical faces.

partment; for forest classification see Davis & Payne, 1982).

Rapid destruction of forest communities on this island is due primarily to selective logging, clear-cutting for plantation, and shifting cultivation. Logging operations began as early as the 1960s but stopped after a few years. In 1989 logging operations (selective logging) began in the northwestern region near Banggi Peak and in the southeastern region near Sabor. From this operation at least six species of commercial trees have been extracted from this island, namely *Intasia palembanica, Shorea* spp., *Hopea sangal, Meiogne viregata, Pantacae* spp., and *Dialium* spp. (Sabah Forestry Department, Kudat). At the time of my field survey, the logging operation near Banggi Peak had been terminated. However, the logging operation near Sabor, and cutting of the mangrove forest throughout the island, was still active. Mangrove wood is extracted primarily for wood pilings and woodchips and is one of the major sources of income for people on this island other than fishing.

Most flat coastal areas have been cleared of primary vegetation for coconut plantations except two or three places north and west of Banggi Peak. Behind the coconut plantations there is a zone of shifting cultivation; this consists of cleared patches planted with tapioca or banana, or patches of secondary forest (belukar) in various stages of regrowth, or areas covered with grass (*Imperata cylindrica*) that have suffered excessive use, leading to soil degradation (Fig. 8). Most of the grasslands are large and liable to burn when there has been no rain for some weeks.

Balambangan Island

More than 40% of the coastal area is covered by mangrove forest, with *Rhizophora mucronata* as the dominant species (Sabah Forestry Department, Vegetational Map, 1972). Mangrove covers coastal areas in the north and southeast. Unlike Banggi, flat coastal areas on this island are not planted with coconut, except for two areas at the most southern tips near Sinai and east near Selamat, but rather are cleared for tapioca and banana. Further inland, especially in the east, west, and north, there is evidence of shifting cultivation and human habitation in the past. The worst areas

FIG. 6. Mangrove forest at trapping Site C2 (Paramuan) on Malawali Island. As on most of the other islands, cutting of mangrove forest for pilings and woodchips was still active on this island. The mangrove forest at this site had recently been selectively logged, forming a large canopy opening.

are near Tanjung Periok in the northeast and Padang in the north, where nothing is visible except open grassland (*Imperata cylindrica*) with patches of *Casuarina nobolis* toward the shore. These areas have been major human habitation sites since the 1770s, when the East India Company Post was set up in 1773. Later, during World War II, it was used as a Japanese Army post (Teo & Sullivan, 1988).

Primary lowland forest in the south and center of this island is still intact and dominated by *Shorea* sp., *Knema* sp., *Gluta* sp., *Calamus* sp., and *Gnetum laurifolium* (Omar et al., 1984). Several timber species were removed during a roughly 1-year logging operation in 1989 on the east coast of the island. The commercial timber species have been reported to be the same as on Banggi Island. Only in the southern portion of this island, where disturbance is least, has a forest reserve been created, the Balambangan Forest Reserve (Forest Reserve Class III), near Kuak Simpol. This reserve covers an area of about 371 ha and includes a small portion of mangrove forest along its eastern edge.

Malawali Island

On Malawali there is clear zonation of vegetation extending from the shore inland. The majority of Malawali's coastal areas are covered by mangrove, except for two sandy beaches, at Paramuan on the southwest coast and at Matalantak on the east coast. Behind the mangrove forest is a narrow band of native shore flora dominated by *Casuarina nobolis.* Inland, there is primary vegetation comprised of *Artocarpus* sp., *Knema* sp., and *Aridisia* sp., except near the south coast, where there is open grassland (*Imperata cylindrica*). There are also patches of rattan (*Calamus* sp.) shrub in the north and patches of small crawling bamboo (*Schizostachyum* sp.) in the west. Only two species of commercially important trees are found on this island, *Dipterocarpus verrutosus* and *Ceriops tagal.*

Molleangen Island

About 75% of this island is covered by coconut plantation that was begun in the early 1950s. The

FIG. 7. View of Molleangen Island from the south. Note that three-quarters of this island is flat, and only a small portion of the island at the southeast is slightly elevated, with the highest peak at 120 m.

only forest remaining occupies an elevated area in the southeastern part of the island (Fig. 9). There are no mangrove or commercial timber species found on this island. Tree species are represented by typical secondary forest trees such as *Pterospermum diversifolium, Mollotus paniculatus,* and *Polyathia microtus.*

Methods

Banggi, Balambangan, Malawali, and Molleangen islands were each visited at least twice within a 5-month period between January and June 1991. Two intensive trapping and netting sessions, at two different sites, and day and night visual surveys were made on foot on each island. Trapping and netting were carried out in primary and secondary lowland forest on each island. Day and night visual surveys included most island habitats: primary lowland forest, secondary lowland forest, primary mangrove forest and secondary mangrove forest (except on Molleangen), plantation (e.g., coconut and tapioca plantation), and grassland (e.g., *Imperata cylindrica,* except on Molleangen Island, and *Staria* sp., only on Banggi Island). Trapping, netting, and visual surveying efforts for both volant and nonvolant mammals were similar on each island; on each island, trapping was about 1,000 trap-nights, bat netting was about 45 net-nights, bat trapping with a harp trap was about 7 trap-nights, and day and night surveys were 20–30 hours (Tables 1 and 2).

Records of nonvolant small mammals on these four islands were established from trapping with Victor snap traps (ca. 45%), local cage traps (30 × 15 × 15 cm, ca. 40%). Sherman live traps (ca. 10%), Museum Special snap traps (ca. 4%), and pitfall traps (ca. 1%). Traps (except pitfall traps) were set 25 to 50 traps in a line at 10- to 15-m intervals; about 85% were placed on the ground and 15% above ground on fallen logs or large vines. Traps were rebaited every day after dawn and in late afternoon, either with banana or with fresh fried coconut coated with peanut butter (except for a few Museum Special traps, which were baited with either earthworms or grasshoppers). Traps

FIG. 8. View of the flat coastal area near Karakit, Banggi Island. Most flat coastal areas on Banggi Island have been cleared for coconut plantations or as a result of shifting cultivation. An area of shifting cultivation is either planted with tapioca or banana, or left unmanaged for several years and replaced by patches of secondary forest (belukar) or grass (*Imperata cylindrica*).

were checked each morning soon after dawn and in early evening, and they were run for three to four consecutive nights.

Bats were caught in either mist nets or double-bank harp traps (Tuttle, 1974; Tiedmann & Woodside, 1978; Payne et al., 1985; Francis, 1989). Mist nets were set on ridgetops and across trails and streams in primary and secondary lowland forest and in plantations next to forest. They were tended continuously for three to four hours following early dusk, then left open until dawn. Nets were run for three to five successive nights at each netting spot. Netting success was calculated based on three consecutive netting nights. Harp traps were used during the second field session and set across small trails or adjacent to small streams in primary and secondary lowland forest. The trap was moved to a different spot each night, and bats were removed only at dawn. In this survey, I caught no fruit bats in the harp trap. One specimen (*Kerivoula hardwickii*) was caught by hand in primary forest on Banggi Island.

Diurnal and nocturnal surveys were made on foot over roads, trails, and forest transects of most of the island habitats. The mammal species that are difficult to catch in traps or to identify by sighting in the wild, mostly the sciurids (i.e., *Ratuffa affinis* and *Petaurista petaurista*), lorises, tarsiers, and deer, were sampled by shooting.

About 45% of the specimens of nonvolant mammals and 98% of the bat specimens were prepared in fluid and the rest either as skeleton, skull only, or skin with skull. Prepared specimens have been housed at the Zoology Museum, Universiti Kebangsaan Malaysia Sabah Campus (UKMS), and the Field Museum of Natural History in Chicago (FMNH).

External measurements, weights, and reproductive information were gathered in the field on fresh animals. On autopsied animals, testes length and width and embryo length, measured as crown-to-rump length (CRL), were taken. The reproductive status of each specimen was estimated. "Adults" were defined as mature, fully grown, and currently

FIG. 9. View of Molleangen Island from the southeast. This is the only forest remaining on this island. Trapping was done at two sites on this island, Site D1 at the north and Site D2 at the south.

or previously breeding individuals with well-developed reproductive organs (nipples or testes). "Subadults" were large young, not fully grown, but in adult pelage. Female subadults were either in estrus or breeding for the first time. The testes of subadult males were smaller than in adult males. "Juveniles" were young, not fully grown, conspicuously smaller than adult and subadults, dull in pelage coloration, and not showing evidence of breeding (DeBlase & Martin, 1974).

Cranial measurements were made on mature/adult specimens with digital calipers graduated to 0.01 mm. Mature/adult specimens were those with fully erupted teeth and well-fused cranial sutures (DeBlase & Martin, 1974). The measurements are defined as follows: condylobasal length, posterior edge of condyle to anterior edge of premaxilla; zygomatic breadth, greatest distance between zygomatic arches; interorbital breadth, least distance dorsally between orbits; mastoid breadth, greatest width of skull between mastoid processes; postorbital width, least distance across top of skull posterior to postorbital process; nasal length, anteriormost to posteriormost point of nasal bone at midline; nasal breadth, greatest width across nasal bones; rostral length, anterior tip of premaxilla to anteriormost portion of orbit, in the infraorbital foramen; palatal length, posterior base of first incisor to posterior edge of palate at midline; palatal breadth at M^3, alveolar distance between third upper molars; postorbital length, posteriormost point of orbit or temporal fossa to posteriormost point of occipital bone; rostral depth, least dorsoventral distance from the point where the maxillary–premaxillary suture crosses the midline on the ventral surface of the rostrum; molariform toothrow, greatest length of molar toothrow; labial palatal breadth at M^1, distance between labial edges of first molar; and diastema length, alveolar distance between last incisor present and first cheek tooth present.

Identification of each species captured by trap, mist net, or firearm was based on Payne et al. (1985) and Medway (1965, 1977). Comparisons of individual specimens were made at the Field Museum of Natural History, Chicago, and at the Zoology Department, National University of Singapore.

TABLE 1. Total individuals, trap-nights, number of species, and percent trapping success of small mammals caught in primary and disturbed forest on Banggi, Balambangan, Malawali, and Molleangen islands from January to June 1991.

Island	Primary	Disturbed	Total
Total individuals			
Banggi Island	199	66	265
Balambangan Island	127	71	198
Malawali Island	190	39	229
Molleangen Island	49	28	77
Trap-nights			
Banggi Island	765	200	965
Balambangan Island	778	280	1058
Malawali Island	516	424	940
Molleangen Island	739	219	954
% Trapping success			
Banggi Island	24.6	31.6	25.9
Balambangan Island	17.7	22.9	19.0
Malawali Island	25.6	27.8	26.7
Molleangen Island	8.4	15.4	9.7
Number of species			
Banggi Island	9	9	9
Balambangan Island	9	6	9
Malawali Island	6	5	6
Molleangen Island	2	2	2

TABLE 2. Total trap-nights and net-nights, and percent netting success of fruit bats on Banggi, Balambangan, Malawali, and Molleangen islands from January to June 1991. Netting success was calculated based on three consecutive netting nights.

Session	Banggi	Balambangan	Malawali	Molleangen
Bat trap-nights				
Session 1	0	0	0	0
Session 2	8	7	6	6
Total	47	45	44	44
Net-nights				
Session 1	10	15	10	19
Session 2	37	30	34	21
Total	47	45	44	44
% Netting success				
Session 1	12.83	3.17	22.67	6.5
Session 2	3.12	1.44	1.62	4.8
Total	3.93	5.30	2.13	4.62

Study Sites

Two sites were chosen for small mammal trapping and bat netting and trapping on each island. The sites were chosen based on the availability of primary forest habitats and the areas most accessible either from the sea or by land. The primary focus was to select the area near the highest peak on each island and to include as many habitats as possible. This was crucial, because my primary objective was to obtain the maximum number of mammal species on these islands. The first trapping session was carried out during the dry season, between February and mid-April, and was followed immediately by the second session, which terminated in June 1991. Study sites and the date of visit for each island are summarized in Table 3.

Banggi Island

Wak-wak (Site A1), an area at the southern tip of Banggi Island (Fig. 2) and part of the Karakit Forest Reserve (24 ha), was visited for 6 days from 8 February to 13 February 1991. Trapping was done at 10 to 60 m elevation in primary lowland forest; netting was conducted along the interface between primary lowland forest and mangrove forest at 10 m elevation. Primary dipterocarp forest consisted of tall canopy trees ranging from 20 to 25 m in height, with diameter at breast height (DBH) from 0.5 to 0.75 m and moderate buttress development. The forest had a broken canopy at 10–15 m, with the lowest canopy at 10 m. Undergrowth was very dense, including saplings, rattans (*Calamus* spp.), and palms. Moss and canopy epiphytes were very uncommon, but woody vines, usually thin and short, were moderately common. The ground was completely covered by leaf litter and several centimeters of humus, thickest at lower elevations. Large and small carbonate outcrops, and old and new fallen logs of 10–30 cm DBH, were extensively distributed throughout the area, especially at the upper elevations. Abundant large fallen logs implied that occasional heavy windstorms occurred, possibly during the southeast monsoon.

Kalangkaman (Site A2), located southeast of Banggi Peak (Fig. 2), is part of the Banggi Forest Reserve (11,206 ha). It was visited for 7 days, from 26 April to 2 May 1991. Trapping and netting were done in primary forest (ca. 50%), secondary forest that had been logged in the early 1960s (ca. 30%), and coconut plantation (ca. 20%). About 30% of trapping effort in primary forest was concentrated in areas along a shallow river. The primary forest

TABLE 3. Selected study sites and dates of visits on Banggi, Balambangan, Malawali, and Molleangen islands.

Island/Site	Elevation	Date of visit
Banggi		
Wak-wak (Site A1)	10–60 m	8 to 13 February 1991
Kalangkaman (Site A2)	100–350 m	26 April to 2 May 1991
Balambangan		
Selamat Darat (Site B1)	10–50 m	8 to 13 March 1991
Kuak Simpol (Site B2)	20–90 m	10 to 16 May 1991
Malawali		
Paramuan (Site C1)	30–40 m	22 to 29 March 1991
Tanjung (Site C2)	30–40 m	24 to 30 May 1991
Molleangen		
South (Site D2)	30 m	22 to 28 February 1991
North (Site D1)	30 m	7 to 14 April 1991

trapping and netting were done only between 100 and 350 m elevation because the area above 400 m elevation was inaccessible (very steep and covered with huge boulders). Above 350 m, trees were rarely greater than 15 m in height, and they were mostly covered by mosses and epiphytes. At the summit, trees were widely spaced, with dense understory vegetation, including grasses, ferns (*Dipteria* spp. and *Gleichenia* spp.), pitcher plants (*Nepenthes* spp.), and orchids. Canopy trees in primary dipterocarp forest between 100 and 400 m elevation ranged from 20 to 25 m in height, with DBH from 0.30 m to more than 0.60 m. Most trees were not buttressed, and the canopy was closed. Understory plants and woody vines were uncommon, but mosses and canopy epiphytes were present and extensively distributed on dead wood and live trees. Although selective logging had taken place and forest fires had occurred, the area below 100 m still harbored many large dipterocarps more than 28 m in height and 0.6 m DBH. However, the open canopy allowed extensive growth of understory plants such as figs (*Ficus* spp.) and ferns.

Visual surveys and some hunting were conducted at three additional specimen localities on this island. Sabor (Site A3), in the eastern part of the island, included logged forest, with scattered open grassland due to shifting cultivation, and mangrove forest on the coast. Lok Tohok (Site A5), in the southern part of the island and about 3 km north of Wak-wak, was covered with mixed grass and old unmanaged coconut plantations, with scattered remnants of forest trees. Karakit (Site A4) is a small town at the southernmost tip of Banggi Island, about 3 km south of Site A1. Several specimens were collected from nearby mangrove forest.

Balambangan Island

Selamat Darat (Site B1), located at the southern end of the island (Fig. 2), was visited from 8 March to 13 March 1991. Small mammals were sampled between 10 and 50 m elevation, with about 65% from secondary forest that had burned in a forest fire during the drought year of 1981 and about 35% from primary forest with little disturbance. Most bat netting was done in the disturbed forest adjacent to primary forest. There were few dipterocarp trees in this forest. Canopy trees were not more than 20 m in height, with DBH not more than 0.40 m, and most trees were not buttressed. In the understory, saplings 10–30 mm in diameter were abundant, implying that the area may have been disturbed in the past by forest fire. Leaf litter did not completely cover the ground, which was dry, with little humus. In the secondary forest, most trees were figs (*Ficus* spp.) ranging from 0.2 to 0.3 m DBH, suggesting recent regeneration, with dense ground-level vegetation dominated by grass and ferns.

Kuak Simpol (Site B2), located east of Balambangan Peak and adjacent to Balambangan Forest Reserve (371 ha) in the southwest (Fig. 2), was visited from 10 May to 16 May 1991. Collecting was conducted between 20 and 90 m elevation in primary forest with little disturbance. The canopy was very dense, with the lower canopy level at 10–

15 m. Canopy trees had diameters up to 1 m DBH and ranged from 20 to 25 m in height. Woody vines, some very long and large, and canopy epiphytes were very common, but mosses were not present. Ground-level vegetation was very sparse. Leaf litter was very thick and covered most of the small carbonate outcrops on the ground. Large carbonate outcrops were distributed sporadically, especially on the hilltops, making it difficult to set traps and nets on a regular transect.

Malawali Island

A site in the northeast near Tanjung (Site C1) and one in the southwest near Paramuan (Site C1; Fig. 2) were sampled from 22 March to 29 March 1991 and from 24 May to 30 May 1991, respectively. At the southeast site, trapping and mist-netting were done in disturbed forest and old unmanaged coconut plantation. However, at the northeast site, small mammals were sampled in primary forest. Two types of habitats can be distinguished in the primary forest: the habitat dominated by *Casuarina nobolis,* with mixed understory saplings 10–20 mm in diameter, pandan, rattans (*Calamus* spp.), and climbing bamboo (*Schizostachyum* spp.), and the habitat in which tall tree species ranged from 15 to 20 m in height with DBH from 0.2 to 0.4 m. In the latter habitat, canopy cover was moderately open. There was moderate ground cover of tree saplings, ranging from 15 to 25 cm in diameter, with moderate leaf litter cover and humus layer. Although no one now lives on this island, there is evidence of past human habitation. Present human disturbance on the island was associated with occasional collection of rattan palms and felling of mangrove trees near the trapping sites.

Molleangen Island

Habitat on this island was fairly homogeneous, consisting of either coconut plantation or primary forest. Small mammals were sampled at a south site (Site D2) from 22 to 28 February 1991 and at a north site (Site D1) from 7 to 14 April 1991 (Fig. 2). Primary habitat consisted of tall canopy trees, ranging from 15 to 20 m in height and 0.2 to 0.3 m DBH, with moderate buttress development and with a broken canopy at 20–30 m. The understory consisted of small saplings and shrubs, with a thin leaf litter and humus layer. In contrast, the coconut plantation habitat was extensively covered by short grasses and herbaceous dicots.

Accounts of Species

Order Insectivora
Family Soricidae—Shrews

Crocidura fuliginosa—The Southeast Asian white-toothed shrew is a poorly known and rarely seen species that has not been previously reported on any offshore island near Borneo (Medway, 1965, 1977; Payne et al., 1985; Reudi et al., 1990). However, this species has been taken from five offshore islands near Peninsular Malaysia: Dayang Bunting, Tioman, Aur, Redang (Chasen, 1940; Medway, 1977), and Singapore (Yang et al., 1990). It is widespread in Southeast Asia and found in a variety of habitats: lightly wooded areas, open grass and scrub, tall coconut plantation, tall secondary and primary forest in lowland and low hill areas, and rocky and mossy forest in montane areas (Thomas, 1889; Banks, 1931; Allen & Coolidge, 1940; Davis, 1962; Lekagul & McNeely, 1977; Medway, 1977; Payne et al., 1985). On 6 March at about 5 p.m. on Balambangan Island, I saw one individual in a small burrow under an old fallen log, in disturbed forest. The log was about 0.35 m in diameter and 2.5 m long, and was lying on the ground about 5 m from and parallel to a small stream. The ground was very damp and sandy, with thick leaf litter and thick humus.

Only two specimens were taken on Balambangan Island, both at site B1: a female was taken in a Victor snap trap set near a dry stream in primary forest, and a male was taken by a domestic cat from a nearby house. The fact that another single specimen was taken by a domestic cat in a house on Tioman Island (Medway, 1966) suggests that the species may at times be associated with human habitation. Although this species was obtained only on Balambangan Island, I suspect that it also existed on the other islands, because little special trapping effort was made to catch insectivores in this survey, with only about 40 to 50 trap-nights (including pitfall traps and Museum Special snap traps) on each island.

Three subspecies of *C. fuliginosa* have been recognized in recent years on mainland Borneo: *C. f. foetida* in the lowlands, *C. f. kelabit* at the upper elevation in Kelabit upland, and *C. f. baluensis* at the higher elevation of Mount Kinabalu (Thomas,

1898a; Medway, 1977; Reudi et al., 1990). Recently, *C. f. kelabit* and *C. f. baluensis* were separated as a distinct species, *C. baluensis* (Corbet & Hill, 1992).

The present specimens have characteristics of the subspecies *C. f. foetida*: short gray pelage about 3–4 mm at the middle of the back, and tail 60–90% of head and body length (Jenkins, 1982; Medway, 1977). The other two subspecies, now known as *C. baluensis,* can be distinguished at once from *C. f. foetida* by having longer and fluffier back hairs (>8 mm in *C. f. baluensis*) and having a long tail (equal to or greater than length of head and body) in *C. f. kelabit* (Thomas, 1889, 1898a; Lim & Heyneman, 1968; Medway, 1977). External and cranial measurements (Table 4) of single male and female specimens from Balambangan Island fall at the lower range of a series of *C. f. foetida* and *C. f. baluensis* from mainland Borneo (Payne et al., 1985).

Specimens examined—Total 2. Balambangan: Site B1 (2 FMNH).

Order Scandentia
Family Tupaiidae—Tree Shrews

Tupaia gracilis—The slender tree shrew is an endemic Bornean species, found throughout Borneo from lowland forest up to submontane forest and on two offshore islands, Banggi and Karimata (Medway, 1977; Payne et al., 1985; Corbet & Hill, 1992). Only one adult female was caught on Banggi Island by Chasen and Kloss (1931). This specimen has characteristics similar to those of the mainland Borneo subspecies, *T. g. gracilis,* but it differs from *T. g. edarata,* the subspecies from Karimata Island (Medway, 1965, 1977; Payne et al., 1985; Corbet & Hill, 1992). *T. g. gracilis* is larger than *T. g. edarata,* with a hind foot over 40 mm and a slightly larger skull, and it differs in skin coloration, with less russet color present posteriorly on *T. g. gracilis* (Lyon, 1913). In this survey, two adult males and five females were trapped in primary forest at Site A1 on Banggi Island. All specimens were obtained in Victor snap traps baited with fried coconut smeared with peanut butter, set mostly on the ground in primary forest. One adult female captured on 11 February had large nipples and one embryo (CRL = 15 mm). External and cranial measurements (Table 4) are similar to those of the specimen collected by Chasen and Kloss (1931) on the same island, and similar to those reported in other series of specimens collected from mainland Borneo (Lyon, 1913; Chasen & Kloss, 1931; Davis, 1958, 1962; Payne et al., 1985; Corbet & Hill, 1992).

Specimens examined—Total 7. Banggi: Site A1 (7 FMNH).

Tupaia minor—The lesser tree shrew inhabits Peninsular Malaysia, Thailand, Borneo, and Sumatra. It is also found on three offshore islands of Borneo: Banggi, Balambangan, and Laut (Medway, 1977; Payne et al., 1985; Corbet & Hill, 1992). Four specimens from Banggi Island and seven specimens from Balambangan Island were collected by Chasen and Kloss (1931). These specimens have characteristics of the subspecies *T. m. caedis,* a race that is confined to the northeastern part of Borneo. These specimens, however, differ from the other mainland subspecies, *T. m. minor,* by having the upper parts browner and the shoulder stripe wider and whiter (Chasen & Kloss, 1931; Davis, 1958, 1962; Payne et al., 1985). I took seven specimens at Site A2 on Banggi Island; four were caught in snap traps baited with fried coconut coated with peanut butter and set in primary forest, and three in cage traps baited with banana and set in disturbed forest and plantations. Another specimen was shot in primary forest near the shore at Site A1 on the same island. On Balambangan Island, all nine specimens were taken in cage traps baited with banana and set in disturbed forest at Site B1. Two pregnant females and one adult male taken on 12 and 13 March on Balambangan Island were examined: each female carried two embryos, one in each horn of the uterus. The two sets of embryos had CRL of 26 and 33 mm. A male had testes measuring 10 × 5 mm. External and cranial measurements of Balambangan and Banggi specimens (Table 4) are similar to those of specimens collected from mainland Borneo and from the same islands by Chasen and Kloss (1931), as well as a specimen from Banggi Island reported by Lyon (1913).

Specimens examined—Total 17. Banggi: Site A1 (1 FMNH), Site A2 (3 FMNH, 4 UKMS). Balambangan: Site B1 (9 FMNH).

Tupaia tana—This large tree shrew is known only from Sumatra, Borneo, and adjacent offshore islands (Medway, 1977; Payne et al., 1985; Corbet & Hill, 1992). Chasen and Kloss (1931) had sampled 10 individuals from Banggi Island and named them as a new subspecies, *T. t. banguei,* which is one of 8 subspecies known from Borneo and adjacent small islands. Earlier, however, Lyon (1913) referred a single specimen from the same island to *T. t. paitana.* I took 6 females and 13 males on

TABLE 4. Means (± SD) and ranges of selected measurements of adult Soricidae, Tupaiidae, and Cynocephalidae. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Rostral length	Molariform toothrow	Palatal breadth at M^3	N	Total length	Tail length	Hindfoot length	Weight (g)
Crocidura fuliginosa													
Balambangan	m	1	22.24	—	7.12	—	4.04	2.60	1	151.0	54.0	15.0	12.0
			—	—	—	—	—	—		—	—	—	—
	f	1	22.11	—	7.52	—	4.16	2.82	1	144.0	57.0	15.0	12.0
			—	—	—	—	—	—		—	—	—	—
Tupaia gracilis													
Banggi	m	2	35.95	20.22	15.06	15.64	6.71	7.96	2	303.0	169.0	38.0	69.0
			(35.38–36.51)	(20.20–20.24)	(14.90–15.21)	(15.56–15.71)	(6.68–6.74)	(7.94–7.97)		(298–308)	(166–172)	(37–39)	(66–72)
	f	2	34.89	20.14	14.96	14.92	6.68	7.69	3	302.3	159.0	38.7	71.3
			(34.36–35.42)	(19.81–20.47)	(14.89–15.03)	(14.67–15.16)	(6.58–6.77)	(7.57–7.80)		(295–306)	(151–164)	(38–40)	(62–79)
Tupaia minor													
Banggi	m	2	34.73	19.82	14.71	14.56	6.35	7.92	4	284.0 ± 17.0	138.5 ± 25.6	32.8 ± 1.5	52.8 ± 14.38
			(34.00–35.45)	(19.60–20.04)	(14.41–15.00)	(13.89–15.22)	(5.94–6.75)	(7.48–8.36)		(263–301)	(101–158)	(31–34)	(53–67)
	f	2	34.27	19.16	13.76	14.40	6.02	7.39	2	281.0	147.5	31.5	67
			(33.47–35.07)	(18.62–19.70)	(13.40–14.11)	(13.94–14.86)	(5.54–6.49)	(7.24–7.53)		(262–300)	(141–154)	(30–33)	(57–77)
Balambangan	m	4	35.80 ± 0.51	20.33 ± 0.19	14.44 ± 0.24	14.51 ± 0.39	6.27 ± 0.12	16.94 ± 0.55	4	261.0 ± 39.9	144.3 ± 6.07	34.2 ± 1.5	56.5 ± 6.39
			(35.33–36.41)	(20.07–20.51)	(14.16–14.71)	(14.20–14.99)	(6.11–6.41)	(16.28–17.49)		(202–288)	(137–151)	(33–36)	(53–66)
	f	2	35.90	20.25	14.33	14.77	6.47	8.24	2	291.0	151.5	34.5	74.0
			(35.65–36.15)	(20.14–20.35)	(14.14–14.52)	(14.60–14.94)	(6.31–6.62)	(8.19–8.28)		(288–294)	(149–154)	(33–36)	(73–75)
Tupaia tana													
Banggi	m	5	50.49 ± 2.33	25.12 ± 0.91	18.16 ± 0.6	26.98 ± 1.38	8.97 ± 0.23	10.04 ± 0.38	10	342.0 ± 15.8	151.2 ± 9.8	45.2 ± 2.3	174.0 ± 44.8
			(47.27–53.12)	(23.65–26.16)	(17.06–18.93)	(25.24–28.68)	(8.74–9.24)	(9.46–10.51)		(328–363)	(138–165)	(41–48)	(120–240)
	f	3	49.88	24.29	17.89	26.69	8.56	10.26	6	336.3 ± 3.4	147.2 ± 7.1	43.3 ± 1.5	158.3 ± 29.1
			(49.32–51.42)	(24.21–24.57)	(17.90–18.18)	(26.45–26.91)	(8.43–8.63)	(10.20–10.36)		(331–341)	(137–156)	(42–46)	(140–215)
Cynocephalus variegatus													
Balambangan	f	1	63.93	40.54	27.60	29.03	9.29	14.54	1	597.0	237.0	—	850.0
			—	—	—	—	—	—		—	—	—	—

Note: Measurements other than weight are in millimeters.

Banggi Island. Seven were taken in primary forest at Site A1, all in cage traps baited with banana. Twelve were trapped in primary and disturbed forest at Site A2; 6 each were caught in cage traps baited with banana and in snap traps baited with fried coconut and peanut butter. One adult male, taken on 28 April, had testes measuring 6 × 3 mm. Cranial and external measurements (Table 4) of these specimens are identical to those from a series collected by Chasen and Kloss (1931) and a specimen reported by Lyon (1913) from Banggi Island. However, these specimens are smaller than *T. t. paitana,* collected by Chasen and Kloss (1931) and Davis (1962) and reported by Lyon (1913); *T. t. speciosa, T. t. besara,* and *T. t. utara* reported by Lyon (1913); *T. t. chrysura* reported by Gunther (1876); *T. t. nitida,* collected by Chasen (1933); and *T. t. kelabit,* collected by Davis (1958), from mainland Borneo. Although external measurements are almost identical, condylobasal length and zygomatic length are slightly smaller than those for a series of *T. t. kertami* from mainland Borneo (Davis, 1962).

Specimens examined—Total 19. Banggi: Site A1 (3 FMNH, 4 UKMS), Site A2 (8 FMNH, 4 UKMS).

Order Dermoptera
Family Cynocephalidae—Flying Lemur

Cynocephalus variegatus—The flying lemur or colugo is a widespread species on the continental shelf of Southeast Asia. It occurs on several offshore islands near Peninsular Malaysia, including Langkawi, Penang, Pangkor, Singapore, Tioman, Aor, and Perhentian (Medway, 1969), and on islands off the north and east coasts of Borneo (Payne et al., 1985; Corbet & Hill, 1992). *C. v. natunae* is the subspecies known on mainland Borneo and on Banggi Island (Gyldenstolpe, 1920; Chasen & Kloss, 1929, 1931; Medway, 1965, 1977; Payne et al., 1985). I collected one female on Balambangan Island and sighted another individual on Banggi Island. This species might be mistaken for the giant flying squirrel (*Petaurista petaurista*); and I observed an individual feeding on the same *Ficus* tree with several giant flying squirrels at Site A2 on Banggi Island. Its size is similar to that of the giant flying squirrel, but it can be distinguished during a glide by having the membranes enclosing the entire tail. A single adult female specimen was given to me by a farmer who had caught it near Site B2 on Balambangan Island. I was told that the specimen had been kept for the previous 6 months and had given birth to a female baby after about 2 months in captivity. The newborn was kept in captivity with the mother, but it died after about 1½ months. In captivity, the mother was fed with young fig (*Ficus* spp.) leaves. External measurements (Table 4) of the female from Balambangan Island fall within the size range of specimens from mainland Borneo (Payne et al., 1985) and from Banggi Island (Chasen & Kloss, 1929, 1931). Cranial measurements are similar to those of three adults from Banggi Island (Chasen & Kloss, 1929, 1931) and two adults from mainland Borneo (Gyldenstolpe, 1920).

Specimens examined—Total 1. Balambangan: Site B2 (1 FMNH).

Order Chiroptera
Family Pteropodidae—Fruit Bats

Cynopterus brachyotis—The short-nosed fruit bat is a common, widespread species in Southeast Asia, ranging from Burma and Vietnam to Java, Sulawesi, and the Philippines, as well as the Andaman and Mentawi islands (Hill, 1983; Koopman, 1989; Payne et al., 1985; Kitchener & Maharadatunkamsi, 1991; Corbet & Hill, 1992). Kitchener and Maharadatunkamsi (1991) recognized several geographic differences and suggested that several species are present. *C. b. brachyotis* is the only subspecies found on mainland Borneo and on adjacent small islands (Andersen, 1912; Medway, 1977; Payne et al., 1985), as well as in Lower Siam (Thailand) and Peninsular Malaysia (Andersen, 1912; Tate, 1942; Medway, 1969; Lekagul & McNeely, 1977). This species was reported on Balambangan Island by Wells (1977) and on most offshore islands by Payne et al. (1985). It occurs in most habitats, including lower montane forest, lowland dipterocarp forest, mangrove forest, plantations, and gardens (Lim & Heyneman, 1968; Payne et al., 1985). I found them abundant and rapidly caught in mist nets set in disturbed and primary forest on all four islands. I netted more than 75 individuals on each island, but only 10–15% of these were preserved for study. Most individuals were netted in secondary forest and coconut plantations. One pregnant female with large nipples, taken on 8 February at Site A1 on Banggi Island, had a fetus of 12 mm CRL. Another adult female gave birth to a male baby after she was captured in a mist net on 9 February at the same site. The baby had a forearm length of 28 mm, total length of 64 mm, tail of 8 mm, and weighed 10 g. Condylobasal length (Table 5) from a series of specimens from these four islands falls

TABLE 5. Means (± SD) and ranges of selected measurements of adult Pteropodidae. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Orbital length	C^1 to M^3
Cynopterus brachyotis							
Banggi	m	5	28.20 ± 0.88	19.22 ± 0.66	12.13 ± 0.06	12.29 ± 0.27	9.41 ± 0.20
			(27.08–29.14)	(18.52–20.31)	(12.06–12.19)	(12.02–12.67)	(9.18–9.66)
	f	5	27.77 ± 0.95	18.74 ± 0.63	12.02 ± 0.29	12.21 ± 0.29	9.32 ± 0.17
			(26.85–28.76)	(18.05–19.66)	(11.59–12.30)	(11.72–12.46)	(9.14–9.60)
Balambangan	m	6	28.00 ± 0.93	18.98 ± 0.47	11.90 ± 0.37	12.12 ± 0.60	9.41 ± 0.40
			(27.24–29.62)	(18.29–19.53)	(11.42–12.28)	(10.98–12.75)	(8.79–9.96)
	f	4	27.15 ± 0.41	18.70 ± 0.65	12.11 ± 0.20	11.70 ± 0.29	9.17 ± 0.19
			(26.55–27.45)	(17.79–19.28)	(11.94–12.38)	(11.46–12.10)	(8.96–9.37)
Malawali	m	5	28.26 ± 1.31	19.35 ± 0.33	11.96 ± 0.21	12.3 ± 0.59	9.54 ± 0.32
			(26.36–29.91)	(18.88–19.77)	(11.74–12.23)	(11.51–12.70)	(9.05–9.93)
	f	5	27.46 ± 0.60	18.77 ± 0.38	11.88 ± 0.09	12.05 ± 0.31	9.24 ± 0.15
Molleangen			(26.71–28.09)	(18.42–19.28)	(11.73–11.94)	(11.62–12.44)	(9.02–9.39)
	m	4	28.12 ± 0.64	19.16 ± 0.27	11.90 ± 0.30	9.44 ± 0.21	9.31 ± 0.45
			(27.62–29.04)	(18.88–19.46)	(11.47–12.13)	(9.24–9.72)	(8.71–9.76)
	f	4	27.63 ± 0.70	19.25 ± 0.61	11.69 ± 0.19	9.48 ± 0.37	9.36 ± 0.47
			(26.59–28.26)	(18.51–19.76)	(11.47–11.93)	(8.94–9.80)	(8.91–9.92)
Eonycteris spelaea							
Banggi	m	1	33.04	21.16	13.52	12.37	12.02
			—	—	—	—	—
Balambangan	m	4	31.77 ± 0.88	20.76 ± 0.77	13.33 ± 0.24	11.92 ± 0.39	11.52 ± 0.41
			(30.99–32.68)	(19.77–21.62)	(13.08–13.65)	(11.37–12.21)	(11.24–12.12)
Macroglossus minimus							
Banggi	m	1	23.44	14.27	9.95	7.68	7.53
			—	—	—	—	—
	f	3	24.47	13.28	9.76	8.04	8.25
			(24.24–24.93)	(12.91–13.62)	(9.52–9.96)	(7.92–8.31)	(8.05–8.48)
Malawali	m	2	23.22	13.75	9.77	8.08	7.61
			(22.99–23.44)	(13.50–14.00)	(9.64–9.90)	(8.08)	(7.45–7.76)
	f	5	23.63 ± 0.40	12.78 ± 0.21	9.55 ± 0.20	7.62 ± 0.17	8.15 ± 0.29
			(23.02–24.00)	(12.45–12.96)	(9.35–9.84)	(7.41–7.83)	(7.89–8.64)
Molleangen	m	2	23.88	14.59	9.81	8.11	8.29
			(23.29–24.46)	(14.53–14.65)	(9.57–10.05)	(8.04–8.17)	(8.06–8.51)
Rousettus amplexicaudatus							
Banggi	m	2	34.80	22.50	13.66	14.07	12.81
			(34.35–35.24)	(22.29–22.71)	(13.52–13.80)	(13.82–14.34)	(12.76–12.85)
	f	3	35.31	21.64	13.58	13.99	13.06
			(34.96–35.58)	(21.32–21.83)	13.22–14.02	13.89–14.06	(12.70–13.45)
Balambangan	m	1	37.40	22.97	14.71	14.43	—
			—	—	—	—	—
	f	5	34.30 ± 0.39	21.15 ± 0.60	13.21 ± 0.42	13.62 ± 0.54	12.66 ± 0.46
			(33.83–34.91)	(20.28–21.73)	(12.75–13.74)	(12.92–13.77)	(12.27–13.40)
Malawali Molleangen	m	1	34.75	20.50	12.65	13.64	12.63
			—	—	—	—	—
	m	1	36.18	23.17	13.78	14.95	17.78
			—	—	—	—	—
	f	1	33.31	19.77	13.41	12.71	12.55
			—	—	—	—	—

Note: Measurements other than weight are in millimeters.

within the range of Bornean specimens (Payne et al., 1985), and agrees with a series collected from lower Siam and Peninsular Malaysia (Gyldenstolpe, 1916) and a series collected from Kalimantan (Lyon, 1911). External measurements, forearm, tail, and weight (Table 5) are slightly above the range of several series from Borneo (Jentink, 1897; Lyon, 1907a; Andersen, 1912; Payne et al.,

TABLE 5. *Extended.*

Molariform toothrow	Palatal breadth at M^3	Palatal length	N	Total length	Tail length	Forearm length	Weight (g)
6.48 ± 0.14	6.29 ± 0.25	14.26 ± 0.66	9	106.0 ± 5.1	9.8 ± 1.9	67.0 ± 3.7	37.3 ± 4.4
(6.34–6.64)	(5.94–6.51)	(13.50–15.03)		(97–110)	(5–11)	(64–69)	(30–41)
6.47 ± 0.14	6.42 ± 0.18	13.72 ± 0.73	4	103.0 ± 5.1	8.7 ± 1.9	66.0 ± 1.8	35.6 ± 3.6
(6.29–6.69)	(6.17–6.53)	(12.96–14.55)		(101–113)	(7–11)	(63–71)	(33–42)
6.62 ± 0.32	6.16 ± 0.11	13.97 ± 0.66	3	103.0	9.3	68.0	31.7
(6.18–7.06)	(6.02–6.34)	(13.33–15.12)		(101–106)	(8–10)	(67–69)	(30–33)
6.44 ± 0.20	6.11 ± 0.18	13.61 ± 0.15	5	104.0 ± 6.1	9.2 ± 1.3	67.4 ± 1.1	30.0 ± 1.7
(6.26–6.70)	(5.94–6.32)	(13.47–13.82)		(96–112)	(8–11)	(66–69)	(29–33)
6.62 ± 0.20	6.37 ± 0.21	14.09 ± 0.83	6	105.5 ± 4.9	9.5 ± 0.8	66.2 ± 3.3	32.8 ± 1.6
(6.35–6.89)	(6.08–6.66)	(13.27–15.23)		(102–115)	(8–10)	(60–69)	(32–36)
6.44 ± 0.15	6.35 ± 0.17	13.44 ± 0.32	10	103.1 ± 4.5	8.9 ± 2.1	66.9 ± 2.0	35.1 ± 4.8
(6.27–6.65)	(6.20–6.61)	(13.04–13.92)		(94–108)	(6–12)	(64–70)	(27–42)
6.36 ± 0.27	6.36 ± 0.25	14.07 ± 0.39	5	103.0 ± 4.0	9.8 ± 1.8	67.0 ± 1.6	34.8 ± 3.6
(5.98–6.62)	(6.22–6.73)	(13.76–14.65)		(99–109)	(8–12)	(65–69)	(30–40)
6.54 ± 0.30	6.19 ± 0.32	13.81 ± 0.18	5	98.4 ± 4.7	8.8 ± 0.8	65.6 ± 3.1	32.6 ± 2.7
(6.18–6.86)	(5.96–6.65)	(13.59–14.00)		(94–106)	(8–10)	(61–69)	(30–37)
6.04	7.35	17.78	2	119.0	12.5	69.0	53.5
—	—	—		(112–126)	(12–13)	(66–72)	(52–55)
5.60 ± 0.22	7.06 ± 0.28	16.85 ± 0.43	5	115.4 ± 5.2	12.6 ± 0.6	68.2 ± 2.5	48.6 ± 8.1
(5.38–5.89)	(6.82–7.36)	(16.48–17.34)		(107–117)	(11–14)	(64–70)	(39–61)
2.93	5.15	13.01	1	68.0	0	39.0	12.0
—	—	—		—	—	—	—
3.21	5.01	13.20	4	69.5 ± 2.4	0	41.3 ± 1.7	10.9 ± 2.0
(2.96–3.49)	(4.89–5.09)	(12.98–13.83)		(68–73)	—	(39–43)	(8–13)
2.99	4.62	12.74	2	68.0	0	40.5	13.0
(2.83–3.15)	(4.52–4.72)	(12.54–12.94)		(66–70)	—	(40–41)	(12–14)
3.14 ± 0.22	4.80 ± 0.06	13.20 ± 0.30	10	67.3 ± 3.6	0	40.6 ± 0.7	11.6 ± 1.4
(2.89–3.48)	(4.73–4.89)	(12.92–13.62)		(62–73)	—	(40–42)	(10–15)
2.94	5.00	12.89	2	68.0	0	42.5	14.0
(2.72–3.16)	(4.96–5.04)	(12.61–13.16)		(67–69)	—	(41–44)	(14)
7.11	8.13	17.52	2	137.0	16.0	84.5	67.5
(6.80–7.42)	(7.99–8.27)	(16.98–18.05)		(136–138)	(16.0)	(84–85)	(63–72)
6.97	7.07	18.33	2	138.0	14.0	85.0	69.0
(6.91–7.08)	(5.53–7.95)	(18.01–18.93)		(138)	(12–16)	(83–87)	(67–71)
—	—	19.30	1	148.0	18.0	82.0	73.0
—	—	—		—	—	—	—
6.85 ± 0.26	7.57 ± 0.26	17.30 ± 0.28	7	133.0 ± 5.4	16.9 ± 1.1	83.3 ± 3.0	60.9 ± 6.6
(6.66–7.30)	(7.37–7.93)	(7.11–17.76)		(126–142)	(14–20)	(79–87)	(54–74)
6.72	7.77	17.82	1	137.0	14.0	78.0	54.0
—	—	—		—	—	—	—
6.99	7.99	18.57	2	143.5	21.0	89.5	76.0
—	—	—		(139–148)	(18–24)	(89–90)	(74–78)
7.22	7.20	17.42	1	125.0	22.0	73.0	44.0
—	—	—		—	—	—	—

1985), two series from Sarawak (Hill, 1959, 1967), and a series from Kalimantan (Lyon, 1907b).

Specimens examined—Total 67. Banggi: Site A1 (13 FMNH, 11 UKMS). Balambangan: Site B1 (11 FMNH). Malawali: Site C1 (8 FMNH, 3 UKMS), Site C2 (3 FMNH, 4 UKMS). Molleangen: Site D1 (13 FMNH), Site D2 (1 FMNH).

Eonycteris spelaea—The cave nectar bat is a

widespread species ranging from India east to the Philippines, Sulawesi, and the Lesser Sundas (Koopman, 1989; Corbet & Hill, 1992). This species has not been reported on any offshore islands of Borneo. I caught most specimens on Banggi and Molleangen islands in disturbed habitat. Three individuals at Site D2 on Molleangen and one individual at Site A3 on Banggi were caught in mist nets set adjacent to clumps of banana (*Musa* sp.). Another individual was netted in logged forest at Site A2 on Banggi Island. External measurements of Banggi and Molleangen specimens (Table 5) fall within the size range of series from mainland Borneo (Chasen, 1931; Hill, 1959; Payne et al., 1985). Condylobasal length and zygomatic breadth are identical to those for a series from Tapadong, Sarawak (Chasen, 1931).

Specimens examined—Total 7. Banggi: Site A1 (1 FMNH), Site A2 (1 FMNH). Molleangen: Site D1 (1 FMNH), Site D2 (3 FMNH, 1 UKMS).

Macroglossus minimus—The dagger-toothed flower bat is a common, widespread species in Southeast Asia, ranging from Thailand and Vietnam through Malaysia and Sumatra to the Philippines, the Solomon Islands, and Australia (Koopman, 1989; Corbet & Hill, 1992). *M. m. lagochilus* is recorded in most areas on mainland Borneo, but it has not been reported on any offshore islands. I netted 18 individuals on Malawali Island, 5 on Banggi Island, and 2 adult males on Molleangen Island. This species was most common in primary forest at Site A1 and Site A2 on Banggi Island, and at Site D2 on Molleangen Island, but it was common in disturbed forest and banana plantation at Site C1 on Malawali Island. External measurements (Table 5) fall within the size range reported by Payne et al. (1985).

Specimens examined—Total 17. Banggi: Site A1 (1 FMNH); Site A2 (4 FMNH). Malawali: Site C1 (2 FMNH), Site C2 (8 FMNH). Molleangen: Site D2 (2 FMNH).

Pteropus vampyrus—The large flying fox is the largest Bornean bat. It is a common, widespread species that extends from Tenasserim and Vietnam to the Lesser Sundas and the Philippines (Koopman, 1989; Corbet & Hill, 1992). *P. v. natunae* is the only subspecies found throughout lowland coastal areas of Borneo, including two offshore islands at the north, Banggi and Balambangan (Chasen & Kloss, 1931; Payne et al., 1985). Chasen and Kloss (1931) collected one female from Balambangan Island and six juveniles from Banggi Island. I was unable to capture specimens of this species, but I saw a group flying south during a night survey on Balambangan Island near Site B2. According to a local fisherman, there are at least two roosts on Sibogok Island at the east of Banggi Island. Flying foxes on these islands are known to local people as "Kabug" or "Kubong."

Rousettus amplexicaudatus—Geoffroy's rousette has an extensive range from Thailand to the Solomon Islands (Koopman, 1989; Corbet & Hill, 1992). *R. a. amplexicaudatus* is the only subspecies on or near Borneo; it was previously known to roost in caves on the main island of Borneo and Balambangan (Payne et al., 1985). I netted 8 individuals in primary forest on Banggi and Balambangan Island: 5 at Site B2 and 3 at Site A2; and 21 individuals were caught in disturbed habitats on all four islands: 2 at Site A1, 6 at Site B1, 1 at Site C1, 11 at Site D1, and 1 at Site D2. External measurements (Table 5) are similar to those for a series from mainland Borneo (Chasen, 1931; Medway, 1965, 1977; Payne et al., 1985). Cranial measurements (Table 5) are similar to those for a series from Peninsular Malaysia (Rookmaaker & Bergmans, 1981).

Specimens examined—Total 29. Banggi: Site A1 (2 FMNH), Site A2 (3 FMNH). Balambangan: Site B1 (1 FMNH, 5 UKMS), Site B2 (4 FMNH, 1 UKMS). Malawali: Site C1 (1 FMNH). Molleangen: Site D1 (10 FMNH, 1 UKMS), Site D2 (1 FMNH).

Family Megadermatidae—False Vampire Bats

Megaderma spasma—The false vampire bat is a widely distributed species extending from India and Indochina through Sumatra to Java, Sulawesi, and the Philippines (Koopman, 1989; Corbet & Hill, 1992). In Borneo it has been reported to roost in caves and hollow trees. Two subspecies, *M. s. kinabalu* and *M. s. trifolium*, are known on the mainland and on several offshore islands near Borneo, and *M. s. carimatae* has been found only on Karimata Island, off the east coast of Borneo (Chasen, 1940; Medway, 1965, 1977; Payne et al., 1985; Corbet & Hill, 1992). Two adult males were netted in primary forest at Site B2 on Balambangan Island, and four specimens were netted in the understory of primary forest dominated by *Casuarina nobolis* at Site C2 on Malawali Island. External measurements (Table 6) fall within the size range of specimens from Peninsular Malaysia and Borneo (Payne et al., 1985).

There was a total of six specimens examined, from Balambangan, Site B2 (2 FMNH) and Malawali, Site C2 (4 FMNH).

Family Nycteridae—Hollow-faced Bats

Nycteris tragata—The hollow-faced bat is a species distributed from Burma south to Sumatra and Borneo (Corbet & Hill, 1992). This species previously was recognized as *N. javanica tragata* (Chasen, 1940; Medway, 1977; Payne et al., 1985; Corbet & Hill, 1992). This species had not previously been taken from any small offshore island near Borneo (Medway, 1977; Payne et al., 1985; Corbet & Hill, 1992). A single female was captured in a mist net at Site D1 on Molleangen Island. The mist net was set on a small peak in primary forest at about 60 m elevation. External measurements (Table 6) of this specimen fall within the size range of *N. tragata* from Peninsular Malaysia (Payne et al., 1985). Cranial measurements (Table 6) of the same specimen are similar to those of a single adult specimen from mainland Borneo (Davis, 1962).

Specimens examined—Total 1. Molleangen: Site D1 (1 FMNH).

Family Rhinolophidae—Horseshoe Bats

Hipposideros cervinus—The fawn roundleaf bat is a common, widespread species from Southeast Asia to Australia (Payne et al., 1985; Corbet & Hill, 1992). *H. c. labuanensis* is the only known subspecies in Borneo. It is a common cave-roosting bat in Sabah and Sarawak, and it was known from three offshore islands, Balambangan, Labuan, and Matanani (Medway, 1965, 1977; Payne et al., 1985). This species has had a confusing taxonomic history and recently has been split from *H. galeritus* by Jenkins and Hill (1981). Two specimens were captured in a harp trap set in primary forest next to a clump of bamboo at Site A2 on Banggi Island. Nineteen specimens were taken on Balambangan Island: 1 in a mist net set across a shallow stream at Site B1 and 18 in a harp trap in the understory of tall primary forest at Site B2. External measurements (Table 7) of my series from Balambangan Island are similar to those for specimens from mainland Borneo (Payne et al., 1985) and from various localities in Peninsular Malaysia, Borneo, Sumatra, and the Philippines (Jenkins & Hill, 1981). However, two individuals from Banggi Island (Table 7) are slightly larger than the size range given by Payne et al. (1985), but fall within the range of a series reported by Jenkins and Hill (1981). Cranial measurements (Table 7) of bats on both islands are within the range for specimens diagnosed by Jenkins and Hill (1981) as *H. cervinus cervinus,* except that the average

TABLE 6. Means (± SD) and ranges of selected measurements of adult Megadermatidae and Nycteridae. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Orbital length	C¹ to M³	Molariform toothrow	Palatal breadth at M³	Palatal length	N	Total length	Tail length	Forearm length	Weight (g)
Megaderma spasma															
Balambangan	m	1	22.27	14.74	10.58	7.72	8.77	5.14	3.64	7.42	1	80.0	0	58.0	20.0
			—	—	—	—	—	—	—	—		—	—	—	—
Malawali	m	2	20.76	13.51	9.84	6.87	8.05	4.57	3.50	7.17	2	77.5	0	53.5	35.5
			(20.70–20.81)	(13.25–13.76)	(9.29–10.38)	(6.72–7.01)	(7.90–8.20)	(4.57)	(3.45–3.55)	(7.13–7.20)		(76–79)	—	(52–55)	(35–36)
	f	1	21.54	13.38	10.13	6.82	8.36	4.84	3.53	7.35	1	65.0	0	56.0	35.0
			—	—	—	—	—	—	—	—		—	—	—	—
Nycteris tragata															
Molleangen	f	1	19.73	13.64	9.02	7.15	8.30	5.34	6.01	5.95	1	138.0	72.0	50.0	15.0
			—	—	—	—	—	—	—	—		—	—	—	—

Note: Measurements other than weight are in millimeters.

TABLE 7. Means (± SD) and ranges of selected measurements of adult Rhinolophidae. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Orbital length	C^1 to M^3	Molariform toothrow
Hipposideros cervinus								
Banggi	m	1	15.68	10.05	9.37	6.03	5.97	3.99
			—	—	—	—	—	—
	f		15.91	9.98	9.25	5.98	6.05	3.97
			—	—	—	—	—	—
Balambangan	m	4	15.53 ± 0.20	9.81 ± 0.16	7.41 ± 0.20	5.89 ± 0.17	5.79 ± 0.07	3.81 ± 0.08
			(15.39–15.82)	(9.63–9.97)	(7.15–7.57)	(5.68–6.07)	(5.72–5.86)	(3.75–3.92)
	f	5	15.54 ± 0.27	9.82 ± 0.25	7.55 ± 0.18	5.91 ± 0.17	5.81 ± 0.14	3.79 ± 0.08
			(15.26–15.81)	(9.49–10.07)	(7.25–7.75)	(5.64–6.06)	(5.62–6.01)	(3.65–3.85)
Hipposideros diadema								
Banggi	m	3	27.3	17.59	14.34	9.85	11.22	6.86
			(26.46–27.74)	(17.16–18.01)	(14.20–14.61)	(9.63–10.20)	(10.99–11.38)	(6.78–6.97)
	f	5	26.35 ± 0.29	16.71 ± 0.52	13.91 ± 0.39	9.68 ± 0.18	10.83 ± 0.19	6.61 ± 0.16
			(25.90–26.67)	(16.16–17.27)	(13.50–14.35)	(9.51–9.90)	(10.57–11.09)	(6.45–6.82)
Balambangan	m	3	26.86	17.69	14.53	9.70	11.28	6.63
			(26.21–27.49)	(17.31–18.00)	(14.49–14.56)	(9.37–9.90)	(10.23–11.66)	(6.47–6.79)
	f	2	26.57	17.05	14.15	9.25	10.95	6.54
			(25.64–27.50)	(16.42–17.58)	(13.71–14.60)	(8.94–9.55)	(10.59–11.31)	(6.51–6.56)
Hipposideros dyacorum								
Balambangan	m	1	13.41	8.97	8.15	5.09	4.98	3.48
			—	—	—	—	—	—
	f	1	13.58	9.25	7.84	5.16	5.07	3.54
			—	—	—	—	—	—
Rhinolophus acuminatus								
Banggi	m	1	19.57	11.32	10.14	6.43	8.14	5.08
			—	—	—	—	—	—
	f	1	—	10.25	9.48	5.96	7.49	4.90
			—	—	—	—	—	—
Rhinolophus trifoliatus								
Malawali	m	1	18.93	10.97	9.52	5.39	7.67	4.78
			—	—	—	—	—	—

Note: Measurements other than weight are in millimeters.

mastoid breadth of the Balambangan specimens is slightly smaller.

Specimens examined—Total 21. Banggi: Site A2 (2 FMNH). Balambangan: Site B1 (1 FMNH), Site B2 (18 FMNH).

Hipposideros diadema—The diadema roundleaf bat is one of the largest cave-roosting bats in Borneo. It is a widespread species, occurring from Southeast Asia to Australia (Payne et al., 1985; Corbet & Hill, 1992). *H. d. masoni* is the only subspecies known on mainland Borneo, and it has not been reported on any adjacent offshore islands (Payne et al., 1985). I caught nine specimens at sites on Banggi Island and five on Balambangan Island. Ten individuals were caught in mist nets set across streams: seven in primary forest at Site A1 on Banggi Island and three in disturbed habitat at Site B1 on Balambangan Island. External measurements of Banggi and Balambangan specimens (Table 7) fall within the size range reported for specimens from mainland Borneo (Payne et al., 1985), except for tails, which are slightly shorter. Condylobasal length and zygomatic breadth are smaller than those for specimens from various localities in Southeast Asia (Hill, 1963a).

Specimens examined—Total 14. Banggi: Site A1 (2 FMNH), Site A2 (7 FMNH). Balambangan: Site B1 (4 FMNH), Site B2 (1 FMNH).

Hipposideros dyacorum—The least roundleaf bat is a species that initially was known only from Borneo, but it has recently been reported from Peninsular Malaysia (Payne et al., 1985; Hill &

TABLE 7. *Extended.*

Palatal breadth at M^3	Palatal length	N	Total length	Tail length	Forearm length	Weight (g)
4.08	6.02	1	85.0	31.0	51.0	8.0
—	—		—	—	—	—
4.30	5.88	1	84.0	30.0	51.0	8.0
—	—		—	—	—	—
3.94 ± 0.14	5.61 ± 0.12	11	78.3 ± 2.7	26.8 ± 1.7	48.6 ± 1.2	7.7 ± 1.4
(3.73–4.06)	(5.43–5.71)		(77–83)	(24–29)	(47–51)	(6–11)
3.96 ± 0.18	5.48 ± 0.48	7	79.7 ± 2.5	26.3 ± 1.4	48.9 ± 1.1	8.6 ± 1.0
(3.79–4.16)	(5.17–6.34)		(76–83)	(25–28)	(48–51)	(7–10)
7.80	10.79	2	142.0	48.5	82.0	39.5
(7.48–8.10)	(10.09–11.48)		(138–146)	(45–52)	(79–85)	(35–44)
7.58 ± 0.28	10.17	5	138.5 ± 4.4	43.3 ± 2.6	79.5 ± 2.1	35.3 ± 4.0
(7.10–7.82)	(9.89–10.59)		(134–144)	(41–47)	(77–82)	(32–41)
8.07	10.66	2	138.5	50.0	81.0	42.0
(7.92–8.31)	(10.47–10.92)		(134–143)	(50)	(80–82)	(42)
7.95	10.59	2	139.0	46.0	81.0	36.0
(7.74–8.19)	(10.47–10.71)		(133–145)	(45–47)	(78–84)	(32–40)
3.74	4.66	1	65.0	18.0	40.0	6.0
—	—		—	—	—	—
3.90	4.79	1	74.0	18.0	42.0	10.0
—	—		—	—	—	—
4.66	7.66	1	85.0	26.0	49.0	—
—	—		—	—	—	—
4.51	7.02	2	83.0	22.0	48.5	16.5
—	—		(82–84)	(21–23)	(48–49)	(15–18)
4.61	6.17	1	97.0	34.0	50.0	13.0
—	—		—	—	—	—

Zubaid, 1989; Corbet & Hill, 1992). My record is the first from a small offshore island. I caught one adult male and one adult female in a harp trap set in the understory of tall primary lowland forest at Site B2 on Balambangan Island. External measurements (Table 7) fall within the size range of those for a series from mainland Borneo (Payne et al., 1985), but the tail is slightly shorter than the holotype specimen from Sarawak (Thomas, 1902). Condylobasal length, zygomatic breadth, and mastoid breadth are slightly smaller than for specimens from Perlis, Peninsular Malaysia (Hill & Zubaid, 1989), and mainland Borneo (Davis, 1962; Hill, 1963a).

Specimens examined—Total 2. Balambangan: Site B2 (2 FMNH).

Rhinolophus acuminatus—The acuminate horseshoe bat inhabits areas ranging from Laos to Java and Palawan (Payne et al., 1985; Corbet & Hill, 1992). In Borneo, the subspecies *R. a. sumatranus* was reported in Sabah only and has not been reported on any adjacent island (Payne et al., 1985). Four specimens, three adult females and one adult male, were caught in mist nets set in the understory of secondary lowland dipterocarp forest at site A2 on Banggi Island. External measurements (Table 7) fall within the size range of specimens from mainland Borneo (Payne et al., 1985) and Peninsular Malaysia (Hill, 1974). Cranial measurements (Table 7) of these specimens agree closely in size with specimens from Peninsular Malaysia (Hill, 1974).

Specimens examined—Total 4. Banggi: Site A2 (4 FMNH).

Rhinolophus borneensis—The Bornean horseshoe bat has a very limited distribution. Initially it was known only on mainland Borneo and several small adjacent islands: Labuan and Banggi islands off the west and north of Sabah, and Karimata, Natuna, and Serutu islands off the south and east of Kalimantan (Andersen, 1905a, b; Tate & Archbold, 1939). This species later was shown to occur on Con Son Island, off Vietnam, and on Java (Hill & Thonglongya, 1972; Payne et al., 1985; Koopman, 1989; Corbet & Hill, 1992). Specimens collected from mainland Borneo, Labuan Island, and Banggi Island were designated as the subspecies *R. b. borneensis,* with *R. b. spadix* from Karimata, Natuna, and Serutu islands (Andersen, 1905a; Hill & Thonglongya, 1972; Payne et al., 1985). *R. b. spadix* can be separated from *R. b. borneensis* by its very slightly larger ears (Hill & Thonglongya, 1972).

No specimens were collected from these four islands in this survey.

Rhinolophus trifoliatus—The trefoil horseshoe bat is a widespread species, found from northeastern India to Java (Koopman, 1989; Corbet & Hill, 1992). *R. t. trifoliatus,* the only subspecies known from Borneo, is found most commonly in the understory of primary forest (Payne et al., 1985). One adult female was caught in a harp trap set in mangrove forest at Site C2 on Malawali Island. External measurements (Table 7) are similar to those for a single adult male collected by Chasen and Kloss (1931) from Banggi Island and fall within the size range for specimens from mainland Borneo (Chasen, 1931; Tate, 1943; Davis, 1962; Payne et al., 1985) and from Peninsular Malaysia (Davis, 1961). However, cranial measurements (Table 7) are smaller than those of specimens from mainland Borneo (Chasen, 1931; Tate, 1943; Davis, 1962) and from Selangor, Peninsular Malaysia (Davis, 1961).

Specimens examined—Total 1. Malawali: Site C2 (1 FMNH).

Family Vespertilionidae—Common Bats

Kerivoula hardwickii—Hardwicke's woolly bat is widespread in Southeast Asia, including records from several small islands in Indonesia, the Philippines, and China (Payne et al., 1985; Corbet & Hill, 1992). *K. h. hardwickii,* the only known subspecies in Borneo, is found most frequently in the understory of tall forest. Previous records include one adjacent island, Balambangan (Wells, 1977; Payne et al., 1985). One adult male was taken in primary lowland dipterocarp forest at Site A1 on Banggi Island. It was caught by hand in the axil of a leaf on a rattan vine about 1 m above ground at about 11:00 a.m. Three adult males were collected in a harp trap set in the understory of primary forest at Site B2 on Balambangan Island. External measurements of those specimens (Table 8) are identical to those for a series from mainland Borneo (Payne et al., 1985).

Specimens examined—Total 4. Banggi: Site A1 (1 FMNH). Balambangan: Site B2 (3 FMNH).

Kerivoula minuta—The least woolly bat is perhaps the smallest Bornean bat, weighing about 2 g; it occurs only in Peninsular Malaysia, Peninsular Thailand, and Borneo (Medway, 1977; Hill & Francis, 1984; Corbet & Hill, 1992). Payne et al. (1985) reported this species on Balambangan Island.

No specimens were taken in this survey.

Miniopterus australis—The lesser bent-winged bat is a species known from Borneo and Sulawesi east to Australia and the Solomon islands (Koopman, 1989). Two subspecies are found in large numbers in small and large caves in Borneo: *M. a. witkampi,* found on the mainland of Borneo, and *M. a. paululus,* found on Balambangan Island (Payne et al., 1985). Two specimens were netted across a shallow stream in primary forest at Site A2 on Banggi Island. Two specimens were netted in disturbed habitat at Site B1, and more than 60 individuals were caught in a harp trap in the understory of primary forest at Site B2 on Balambangan Island. External measurements of Balambangan and Banggi specimens (Table 8) are similar to those of specimens from mainland Borneo (Chasen, 1931; Hill, 1959; Payne et al., 1985). However, one cranial measurement (Table 8), condylobasal length, is slightly smaller than that for a series from mainland Borneo (Payne et al., 1985).

Specimens examined—Total 55. Banggi: Site A2 (2 FMNH). Balambangan: Site B1 (2 FMNH), Site B2 (21 FMNH, 30 UKMS).

Miniopterus magnater—This is a widespread species ranging from Southeast Asia to Australia (Payne et al., 1985), formerly confused with *M. schreibersii.* It was reported from roosts in a cave on Balambangan Island (Payne et al., 1985), but no individuals were caught in this survey.

Miniopterus schreibersii—The common bent-winged bat is an exceptionally widespread species in Asia, Europe, and Africa (Payne et al., 1985; Corbet & Hill, 1992). A single adult male was netted in selectively logged dipterocarp forest at Site A2 on Banggi Island. Although the specimen is almost identical in appearance to *M. magnater,* forearm length and condylobasal length (Table 8) agree closely with measurements in a series of specimens of *M. schreibersii* from mainland Borneo (Payne et al., 1985).

Specimens examined—Total 1. Banggi: Site A2 (1 FMNH).

Murina cyclotis—The orange tube-nosed bat is a medium-sized insectivorous bat known throughout Southeast Asia, China, and the Philippines (Heaney et al., 1991). *M. c. peninsularis* is the subspecies known in Peninsular Malaysia and Borneo; it is often caught in the understory of lowland dipterocarp forest (Medway, 1969; Payne et al., 1985). I caught one adult male in a harp trap set in the understory of primary forest at Site B1 on Balambangan Island. External and cranial measurements (Table 8) of this specimen agree in size with the range of measurements from a series collected on mainland Borneo (Hill & Francis, 1984; Payne et al., 1985) and from another series of specimens collected in Peninsular Malaysia (Hill, 1963b, 1972), except for condylobasal length, which is slightly smaller than the range reported by Payne et al. (1985).

Specimens examined—Total 1. Balambangan: Site B1 (1 FMNH).

Murina suilla—The lesser tube-nosed bat is a species known only from the continental shelf area of Malaysia and Indonesia, and Nias, an oceanic island west of Sumatra (Koopman, 1989). On Borneo, this species is often found in lowland dipterocarp forest (Payne et al., 1985). I netted one adult male in primary forest along a ridge at 50 m elevation at Site D2 on Molleangen Island. External and cranial measurements (Table 8) of this specimen fall within the size range of specimens from mainland Borneo (Payne et al., 1985).

Specimens examined—Total 1. Malawali: Site D2 (1 FMNH).

Myotis macrotarsus—The pallid large-footed myotis is a cave-roosting species known only from the Philippines and Borneo (Corbet & Hill, 1992). The one subspecies known from Borneo, *M. m. saba,* has been reported in many caves on mainland Borneo and Balambangan Island (Payne et al., 1985). In my survey, I obtained 16 specimens on Balambangan Island; 2 were netted across a dry stream bed at Site B1, and 14 were caught at Site B1 in a harp trap set in the understory of primary lowland forest. External measurements (Table 8) are similar to those for two series from mainland Borneo (Davis, 1962; Payne et al., 1985). Condylobasal length and zygomatic breadth agree in size with a series from mainland Borneo (Davis, 1962).

Specimens examined—Total 16. Balambangan: Site B1 (16 FMNH).

Phoniscus atrox—The gilded groove-toothed bat is a poorly known species restricted to the continental shelf of Southeast Asia. In Borneo, it previously was known only from eastern Sabah. Three individuals were caught in a harp trap in primary lowland forest at Site B2 on Balambangan Island. External and cranial measurements (Table 8) fall within the range of two series of specimens collected on mainland Borneo reported by Payne et al. (1985) and Hill and Francis (1984).

Specimens examined—Total 3. Balambangan: Site B2 (3 FMNH).

Pipistrellus javanicus—The Javan pipistrelle is a widespread species in Southeast Asia, China, and Japan (Payne et al., 1985). *P. j. javanicus* is the only known subspecies in Borneo; it has been reported in Sabah and at Pontianak, west Kalimantan (Payne et al., 1985; Francis & Hill, 1986). In Sabah, this species is frequently caught in the understory of mossy forest (Francis & Hill, 1986). I took one adult female in a harp trap set in mangrove forest adjacent to primary lowland forest at Site C2 on Malawali Island. Cranial and external measurements (Table 8) fall within the range of two series of specimens from mainland Borneo examined by Francis and Hill (1986) and Payne et al. (1985).

Specimens examined—Total 1. Malawali: Site C2 (1 FMNH).

Pipistrellus stenopterus—The narrow-winged pipistrelle has been reported from Peninsular Malaysia, Borneo, the Philippines, and Sumatra (Koopman, 1993). Nine specimens were netted across a small dry stream in disturbed habitat at Site B1 on Balambangan Island. Cranial and external measurements (Table 8) fall within the size range of a series of specimens from Peninsular Malaysia (Payne et al., 1985) and from mainland Borneo (Tate, 1942; Davis, 1962; Francis & Hill, 1986).

Specimens examined—Total 9. Balambangan: Site B1 (9 FMNH).

TABLE 8. Means (± SD) and ranges of selected measurements of adult Vespertilionidae. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Orbital length	C^1 to M^3	Molariform toothrow
Kerivoula hardwickii								
Banggi	m	1	12.36	8.05	7.11	3.62	5.22	2.72
			—	—	—	—	—	—
Balambangan	f	3	12.52	8.18	6.92	3.92	5.35	2.88
			(11.97–12.86)	(7.94–8.43)	(6.40–7.25)	(3.81–4.01)	(5.13–5.49)	(2.75–2.99)
Miniopterus australis								
Banggi	m	1	12.45	7.30	7.22	3.97	4.73	2.88
			—	—	—	—	—	—
	f		—	—	—	—	—	—
			—	—	—	—	—	—
Balambangan	m	5	12.50 ± 0.16	7.34 ± 0.10	7.18 ± 0.11	4.15 ± 0.22	4.98 ± 0.10	2.93 ± 0.07
			(12.33–12.70)	(7.21–7.49)	(7.06–7.33)	(3.88–4.36)	(4.85–5.08)	(2.85–3.02)
	f	5	12.57 ± 0.22	7.27 ± 0.14	7.14 ± 0.08	4.25 ± 0.12	4.94 ± 0.10	2.92 ± 0.11
			(12.28–12.80)	(7.08–7.41)	(7.03–7.21)	(4.12–4.43)	(4.80–5.08)	(2.80–3.07)
Miniopterus schribersi								
Banggi	m	1	15.01	8.45	8.50	5.00	5.90	3.35
			—	—	—	—	—	—
Murina cyclotis								
Balambangan	m	1	15.87	10.33	8.64	5.60	6.00	3.13
			—	—	—	—	—	—
Murina suilla								
Molleangen	m	1	12.93	8.42	7.01	4.45	4.78	2.79
			—	—	—	—	—	—
Myotis macrotarsus								
Balambangan	m	4	17.00 ± 0.21	11.63 ± 0.17	9.38 ± 0.11	5.88 ± 0.08	6.99 ± 0.34	4.19 ± 0.06
			(16.74–17.23)	(11.43–11.81)	(9.26–9.49)	(5.82–6.00)	(6.94–7.02)	(4.10–4.23)
	f	4	17.02 ± 0.21	11.47 ± 0.07	9.15 ± 0.12	5.75 ± 0.10	7.10 ± 0.08	4.23 ± 0.10
			(16.76–17.26)	(11.38–11.54)	(9.01–9.25)	(5.61–5.84)	(6.99–7.16)	(4.10–4.35)
Phoniscus atrox								
Balambangan	m	1	13.40	8.52	7.33	4.50	5.72	2.89
			—	—	—	—	—	—
	f	2	13.20	8.47	7.24	4.32	5.67	2.92
			(13.03–13.36)	(8.21–8.73)	(7.14–7.34)	(4.06–4.40)	(5.56–5.77)	(2.91–2.93)
Pipistrellus javanicus								
Malawali	f	1	11.94	7.96	7.00	4.52	4.31	2.76
			—	—	—	—	—	—
Pipistrellus stenopterus								
Balambangan	m	1	15.90	12.23	10.02	6.66	5.98	3.91
			—	—	—	—	—	—
	f	5	15.14 ± 0.36	11.18 ± 0.17	9.57 ± 0.29	6.20 ± 0.12	5.68 ± 0.18	3.70 ± 0.16
			(14.80–15.64)	(10.95–11.34)	(9.27–9.96)	(6.07–6.30)	(5.58–5.99)	(3.49–3.90)
Pipistrellus vordermanni								
Banggi	m	1	12.44	8.72	7.58	4.90	4.51	3.03
			—	—	—	—	—	—

Note: Measurements other than weight are in millimeters.

Pipistrellus vordermanni—The white-winged pipistrelle is a very poorly known species. The holotype is from Billiton Island. The first specimen from Borneo was from Samsunam, Sarawak (Payne et al., 1985; Francis & Hill, 1986). A male I captured, the second specimen from Borneo (and the first from Sabah), was caught in a mist net set across the road between primary lowland forest

TABLE 8. *Extended.*

Palatal breadth at M^3	Palatal length	N	Total length	Tail length	Forearm length	Weight (g)
2.62	7.15	1	80.0	41.0	32.0	5.0
—	—		—	—	—	—
2.66	6.78	3	87.0	43.0	32.7	4.3
(2.51–2.78)	(6.55–6.93)		(83–90)	(38–47)	(31–34)	(4–5)
2.87	5.70	1	80.0	36.0	36.0	5.0
—	—		—	—	—	—
—	—	1	88.0	38.0	36.0	4.0
—	—		—	—	—	—
2.86 ± 0.08	6.01 ± 0.21	10	85.4 ± 3.4	37.0 ± 2.5	35.3 ± 1.0	5.0 ± 0.5
(2.74–2.97)	(5.81–6.36)		(79–91)	(32–40)	(34–37)	(4–6)
2.70 ± 0.09	5.76 ± 0.25	10	82.1 ± 3.2	36.5 ± 2.9	35.2 ± 1.4	5.1 ± 0.7
(2.55–2.76)	(5.52–6.13)		(78–88)	(30–40)	(32–37)	(4–6)
3.63	6.92	1	107.0	48.0	44.0	11.0
—	—		—	—	—	—
3.10	8.36	1	96.0	41.0	36.0	7.0
—	—		—	—	—	—
2.97	6.74	1	71.0	32.0	31.0	3.0
—	—		—	—	—	—
3.94 ± 0.23	9.11 ± 0.09	6	112.7 ± 4.4	48.5 ± 3.4	46.0 ± 1.1	12.3 ± 1.5
(3.76–4.28)	(9.06–9.24)		(108–118)	(44–52)	(45–48)	(11–15)
3.87 ± 0.04	9.17 ± 0.19	6	113.5 ± 0.8	48.0 ± 3.4	48.0 ± 1.1	14.2 ± 0.8
(3.84–3.92)	(8.94–9.35)		(112–114)	(42–52)	(46–49)	(13–15)
2.59	7.74	1	81.0	40.0	33.0	4.0
—	—		—	—	—	—
2.55	7.30	2	78.5	37.0	33.3	4.0
(2.51–2.59)	(7.15–7.45)		(78–79)	(37)	(33–34)	(3–5)
3.07	5.00	1	79.0	34.0	33.0	5.0
—	—		—	—	—	—
4.61	6.57	1	102.0	40.0	40.0	15.0
—	—		—	—	—	—
4.25 ± 0.14	6.53 ± 0.25	7	106.3 ± 2.9	39.3 ± 1.8	39.0 ± 1.2	14.3 ± 1.2
(4.03–4.36)	(6.33–6.92)		(102–110)	(37–42)	(38–41)	(13–16)
3.20	5.60	1	84.0	33.0	33.0	6.0
—	—		—	—	—	—

and mangrove forest at Site A1 on Banggi Island. Cranial and external measurements (Table 8) of the single specimen are larger than those of the specimen collected from Sarawak (Francis & Hill, 1986). However, the length of the forearm is similar to that of the holotype (Tate, 1942).

Specimens examined—Total 1. Banggi: Site A1 (1 FMNH).

TABLE 9. Means (± SD) and ranges of selected measurements of adult Primates. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylo-basal length	Zygo-matic width	Mastoid width	Orbital length	C^1 to M^3	Molari-form toothrow	Palatal breadth at M^3	Palatal length	N	Total length	Tail length	Forearm length	Weight (g)
Nycticebus coucang															
Banggi	—		—	—	—	—	—	—	—	—	1	339.0	215.0	67.0	94.0
			—	—	—	—	—	—	—	—		—	—	—	—
Tarsius bancanus															
Banggi	m	1	55.38	40.44	33.83	—	20.67	8.36	11.96	18.29		—	—	—	—
			—	—	—	—	—	—	—	—		—	—	—	—
Macaca fascicularis															
Banggi	m	1	101.50	83.20	—	25.00	39.70	—	—	—	1	1,080.0	595.0	133.0	5,600.0
			—	—	—	—	—	—	—	—		—	—	—	—
	f	1	83.40	72.60	—	22.50	33.60	—	—	—	1	905.0	492.0	129.0	3,800.0
			—	—	—	—	—	—	—	—		—	—	—	—

Note: Measurements other than weight are in millimeters.

Family Molossidae—Free-tailed Bats

Cheiromeles torquatus—The naked bat is a species inhabiting Malaysia, Thailand, Sumatra, Borneo, Palawan, and smaller nearby islands. It was reported on Banggi Island by Payne et al. (1985). No specimens were caught in this survey.

Order Primates
Family Lorisidae—Lorises

Nycticebus coucang—The distribution of the slow loris extends from eastern India southward to Java and the eastern Philippines (Fooden, 1991a; Timm & Birney, 1992). Fooden (1991a) reported that this species is found on small Philippine islands off the east coast of Borneo: Tawi-tawi, Simunul, Bangao, and Sanga-sanga islands. The slow loris in Borneo has been described as *N. c. borneanus* (Medway, 1965, 1977). My specimen is the first record of this species on smaller islands north of Borneo; a single adult female was shot at Site A3 on Banggi Island, and several other individuals were sighted on the same island. One individual was observed climbing on a small tree at about 8:00 p.m. at Karakit Forest Reserve, and another individual was sighted at 9:00 p.m. on a tree near the main road to Site A4, about 3 km north of Site A1. Local people reported that this species can be found throughout the island. External measurements were not taken, but condylobasal length and zygomatic width of the adult female specimen (Table 9) are far larger than in a young adult male specimen obtained by Davis (1962) from mainland Borneo.

Specimens examined—Total 1. Banggi: Site A3 (1 FMNH).

Family Tarsiidae—Tarsiers

Tarsius bancanus—The western tarsier previously was known only from Borneo, southern Sumatra, and the nearby islands of Bangka, Karimata, Billiton, and Sirhassan (Payne et al., 1985). One adult female, tentatively referred to *T. b. bancanus*, is the first record from the offshore islands of Borneo; it was shot during a night survey on 19 June at Site A3 on Banggi Island in old logged forest. During that survey, in the same habitat, three other individuals were sighted. Based on field surveys and reports from natives, the species is found only in the northeastern part of Banggi Is-

land, especially in selectively logged habitat and old secondary growth habitat. External measurements (Table 9) of a single specimen fall within the size range of those specimens from mainland Borneo reported by Payne et al. (1985), Musser and Dagosto (1987), and Davis (1962). No cranial measurements are available due to the badly damaged skull.

Specimens examined—Total 1. Banggi: Site A3 (1 FMNH).

Family Cercopithecidae—Old World Monkeys

Macaca fascicularis—The long-tailed macaque is a widespread species in Southeast Asia, and it is common on offshore islands. This is one of the most abundant large mammal species on offshore islands near Borneo, and it occupies most coastal habitats (Medway, 1965, 1977; Payne et al., 1985). During my field survey, a group of macaques was observed in mangrove forest at Site C2 on Malawali Island. A young adult male macaque was found dead on top of a small ridge at Site D1 near the southeast coast of Molleangen Island, and a group was observed feeding on coconuts at the same site. I saw only one macaque during my survey on Balambangan Island, in mangrove forest at Site B1. However, on Banggi Island macaques were very common, not only in mangrove forest, but also in secondary forest and plantations. Chasen and Kloss (1931) obtained specimens only from Banggi Island. In my recent survey I sampled two specimens from Banggi Island: an adult female was shot about 3–4 km further inland from Site A3 on 19 June, and an adult male was shot in mangrove forest at Site A4 on 22 June. External and cranial measurements of these two specimens (Table 9) are almost identical to those of an adult male specimen collected by Chasen and Kloss (1931) from Banggi Island and fall within the size range reported by Fooden (1991b), Payne et al. (1985), and Davis (1962).

Specimens examined—Total 2. Banggi: Site A5 (1 FMNH), Site A3 (1 FMNH).

Order Pholidota
Family Manidae—Pangolins

Manis javanica—The pangolin or scaly anteater is a species inhabiting Southeast Asia, including some adjacent islands, but not reported on any offshore islands near Borneo (Payne et al., 1985). An individual was observed roaming in selectively logged forest during the field survey on 19 June at Site A3 on Banggi Island. Another individual was also reported shot by a hunter at the same area a month before.

No specimens are available.

Order Rodentia
Family Sciuridae—Squirrels

Callosciurus prevostii—Prevost's squirrel is a widespread species from southern Thailand, Peninsular Malaysia, Sumatra, Singapore, Borneo, and many adjacent small islands (Medway, 1969; Heaney, 1978; Yang et al., 1990). Chasen and Kloss (1931) took five specimens each from Banggi Island and Balambangan Island. On the basis of skull size, which is slightly smaller than among subspecies from the mainland, Chasen and Kloss (1931) described Banggi and Balambangan specimens as separate subspecies, *C. prevostii caedis.* In this survey, two specimens (one adult male and female) were shot in a coconut plantation near Site A1 on Banggi Island. On Balambangan Island, 14 specimens were obtained in live traps at Site B1: 6 were caught adjacent to tapioca plantations and 8 in disturbed forest. Based on my field observations, on Banggi Island the species was common in coconut plantations and fringing forest, and on Balambangan Island it was most common in tapioca plantations and disturbed habitats. Cranial and external measurements of Banggi and Balambangan specimens (Table 10) are almost identical to those of specimens collected by Chasen and Kloss (1931) from the same islands but slightly smaller than those of specimens from mainland Borneo (Chasen & Kloss, 1931; Davis, 1961; Heaney, 1978; Payne et al., 1985).

Specimens examined—Total 16. Banggi: Site A1 (2 FMNH). Balambangan: Site B1 (10 FMNH, 4 UKMS).

Callosciurus notatus—Like *C. prevostii,* the plantain squirrel is also a widespread species on the Sunda Shelf, including small islands such as Singapore, Penang, Tioman, and Perhentian. On small islands near Borneo it is known only on Malawali Island. Chasen and Kloss (1931) collected nine specimens from this island and recognized them as a distinct subspecies, *C. n. malawali.* Nine of my specimens were caught in cage traps set about 1 m above the ground, either on trees or on fallen logs, one in a snap trap set on a tree vine, and three in cage traps set on the ground.

TABLE 10. Means (± SD) and ranges of selected measurements of adult Sciuridae. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Rostral length	Orbital length
Callosciurus prevostii							
Banggi	m	1	—	32.84	—	10.82	15.38
			—	—	—	—	—
	f	1	47.63	32.62	22.77	11.29	16.12
			—	—	—	—	—
Balambangan	m	3	47.49	31.18	21.40	22.25	15.88
			(47.00–47.91)	(30.46–31.54)	(20.90–22.05)	(21.91–22.59)	(15.61–16.10)
	f	3	47.77	31.17	21.56	22.35	15.91
			(46.77–48.57)	(30.39–31.70)	(21.14–21.88)	(21.44–22.90)	(15.34–16.37)
Callosciurus notatus							
Malawali	m	2	44.86	28.72	20.77	10.42	19.72
			(44.49–45.22)	(28.33–29.11)	(20.41–21.13)	(10.40–10.44)	(19.48–19.96)
	f	1	43.82	27.96	20.24	10.36	15.04
			—	—	—	—	—
Petaurista petaurista							
Banggi	m	1	61.77	45.69	31.70	20.09	25.69
			—	—	—	—	—
	f	1	61.88	44.20	32.36	19.96	24.81
			—	—	—	—	—
Sundasciurus lowii							
Banggi	m	1	34.72	22.22	16.43	15.74	12.18
			—	—	—	—	—
	f	3	34.39	21.64	16.07	15.41	11.58
			(32.45–36.25)	(20.41–22.72)	(15.28–16.98)	(14.49–16.63)	(11.31–11.93)
Balambangan	f	2	34.78	22.02	16.44	15.91	12.50
			(34.67–34.88)	(21.92–22.11)	(16.35–16.52)	(15.86–15.95)	(12.04–12.56)

Note: Measurements other than weight are in millimeters.

Of these, four were trapped in primary forest, four in an old coconut plantation, and five in disturbed forest. Cranial and external measurements (Table 10) are similar to those for specimens from mainland Borneo (Davis, 1962; Payne et al., 1985). However, the condylobasal length is slightly smaller than that of a series of specimens collected by Chasen and Kloss (1931) from the same island.

Specimens examined—Total 13. Malawali: Site C1 (4 FMNH, 5 UKMS), Site C2 (1 FMNH, 3 UKMS).

Exilisciurus exilis—The plain pygmy squirrel is known only from mainland Borneo and Banggi Island (Chasen & Kloss, 1931; Heaney, 1985a; Payne et al., 1985). On mainland Borneo, this species occurs most often in tall and logged dipterocarp forest; it is recognized as *E. e. exilis,* differing slightly in coloration from the subspecies *E. e. retectus,* from Banggi Island (Chasen & Kloss, 1931; Payne et al., 1985). Although Chasen and Kloss (1931) took four specimens, I did not catch or sight any individuals on this island, perhaps because their density is now very low. It is possible that the species is extinct on Banggi Island, but this is unlikely since a large area of primary habitat is still intact on the island.

No specimens are available.

Petaurista petaurista—The red giant flying squirrel is one of the largest flying squirrels in Borneo. It is widespread in Asia, including two small offshore islands near Peninsular Malaysia, Tioman and Penang (Medway, 1969), but it has not been reported on any offshore islands near Borneo. Two specimens, one adult male and one adult female, were shot at Site A3 on 19 June, the first records from Banggi Island. This species is very abundant in the northwestern and northeastern portions of Banggi Island. During a night survey on 28 April, I saw nine individuals feeding on wild fig fruit (*Ficus microcarpa*) at Site A2, and on 19 June I saw two individuals at Site A3. Only cranial measurements (Table 10) are available; these measurements fall within the size range of two subspecies from mainland Borneo (Payne et al., 1985), but condylobasal length is smaller than that of two

TABLE 10. *Extended.*

Molariform toothrow	Palatal breadth at M^3	Diastema length	N	Total length	Tail length	Forearm length	Weight (g)
7.30	11.74	12.44		—	—	—	—
—	—	—		—	—	—	—
7.46	12.69	11.96	1	432.0	193.0	53.0	350.0
—	—	—		—	—	—	—
6.92	12.03	12.22	4	413.8 ± 4.8	200.8 ± 4.8	50.8 ± 1.3	275.8 ± 34.0
(6.88–6.95)	(11.67–12.34)	(12.15–12.32)		(408–419)	(196–206)	(49–52)	(260–320)
6.99	12.20	12.45	4	410.3 ± 9.5	196.5 ± 8.6	48.8 ± 3.6	238.8 ± 18.9
(6.88–7.30)	(11.88–12.44)	(12.11–12.96)		(403–423)	(191–208)	(44–52)	(260–305)
6.05	10.79	11.89	6	364.2 ± 6.6	174.0 ± 7.9	47.7 ± 2.9	197.5 ± 17.9
(6.03–6.06)	(10.72–10.85)	(11.70–12.08)		(354–371)	(161–182)	(42–50)	(165–220)
6.07	10.40	11.21	4	352.0 ± 11.4	154.5 ± 15.2	44.6 ± 2.9	192.5 ± 9.6
—	—	—		(341–365)	(133–168)	(41–47)	(180–200)
10.10	16.27	13.06	—	—	—	—	—
—	—	—		—	—	—	—
9.97	16.94	14.89	—	—	—	—	—
—	—	—		—	—	—	—
5.00	8.64	9.74	1	229.0	94.0	37.0	80.0
—	—	—		—	—	—	—
5.20	8.66	9.29	4	224.5 ± 17.5	85.5 ± 10.0	34.8 ± 0.5	82.0 ± 12.9
(5.11–5.35)	(8.45–9.06)	(8.95–9.51)		(206–248)	(76–96)	(34–35)	(63–91)
4.76	8.53	9.65	1	208.0	63.0	33.0	80.0
(4.72–4.79)	(8.51–8.54)	(9.60–9.70)		—	—	—	—

P. p. rajah specimens from Kalabakan, Sabah (Davis, 1962).

Specimens examined—Total 2. Banggi: Site A4 (2 FMNH).

Ratufa affinis—This is the world's largest tree squirrel. It is widely distributed throughout Southeast Asia, including several Bornean offshore islands: Laut, Penebangan, Sebuku, and Banggi (Medway, 1977; Payne et al., 1985). A single adult male was collected by Chasen and Kloss (1931). My survey revealed that they were very abundant in the northwestern and the northeastern parts of Banggi Island; one adult male was shot at Site A3, and several were seen in selectively logged areas at Site A2 feeding on twigs and wild fruits at about 10–15 m from the ground. However, none were observed in the south near the Karakit Forest Reserve. Only three cranial measurements were taken: rostral length, 25.4 mm; orbital length, 23.7 mm; and diastema length, 14.9 mm; these measurements fall within the size range for specimens from mainland Borneo reported by Payne et al. (1985). Because of incomplete cranial and external measurements, no comparisons were made to specimens collected by Chasen and Kloss (1931) from the same island or from mainland Borneo. However, Chasen and Kloss (1931) suggested that the subspecies *R. a. banguei,* from Banggi Island, is smaller and has much darker upperparts than the subspecies *R. a. sandakanensis,* from adjacent mainland Borneo.

Specimens examined—Total 1. Banggi: Site A3 (1 FMNH).

Sundasciurus lowii—Low's squirrel is known only from Peninsular Malaysia, Sumatra, Borneo, and smaller adjacent islands. This species has been found in tall and secondary lowland forest throughout mainland Borneo, and also in hills up to 1400 m in the Kelabit upland (Lyon, 1911; Gyldenstolpe, 1920; Davis, 1958, 1962; Payne et al., 1985). Two subspecies were distinguished earlier from Borneo: *S. l. lowii,* on mainland Borneo (Thomas, 1892), and *S. l. bangueyae,* from Banggi Island (Thomas, 1910). Based on five specimens

collected from Banggi Island, Chasen and Kloss (1931) concluded that specimens from Banggi Island are indistinguishable from the mainland form. I captured two specimens of this species in cage traps set on the ground in disturbed forest at Site B1 on Balambangan Island. Five were obtained on Banggi Island: two in cage traps set on the ground at Site A2 in primary forest and coconut plantation, two in snap traps, and one in a cage trap set on the ground in primary forest at Site B2. Cranial and external measurements of Banggi and Balambangan (Table 10) specimens are similar to those of specimens from mainland Borneo (Thomas, 1892; Lyon, 1911; Gyldenstolpe, 1920; Chasen & Kloss, 1931; Davis, 1958, 1962; Payne et al., 1985), but they are slightly larger than those of the series of five specimens from Banggi Island collected by Chasen and Kloss (1931).

Specimens examined—Total 7. Banggi: Site A1 (2 FMNH, 1 UKMS), Site A2 (2 FMNH). Balambangan: Site B1 (2 FMNH).

Family Muridae—Rats and Mice

Maxomys surifer—The red spiny rat is a common species on both large and small islands in Southeast Asia, including small islands off the north, south, and west coasts of Borneo. Specimens of this rat from Banggi, Balambangan, and Malawali islands were originally referred to the name *Rattus* (*Maxomys*) *panglima* by Chasen and Kloss (1931). Medway (1977) pointed out that they are members of the species *Maxomys surifer*; this was confirmed by Musser et al. (1979). The use of the name *Maxomys surifer panglima* by Payne et al. (1985) is in error. Rats from Banggi, Balambangan, and Malawali islands have slightly darker coloration and a shorter tail than the subspecies from mainland Borneo, *M. s. bendahara*. On mainland Borneo, this species is found in forest, grassland, and rice fields (Musser et al., 1981; Payne et al., 1985). I found this species most often in primary forest; three out of six specimens were taken in primary forest on Malawali Island, 34 specimens in primary forest and six in disturbed forest on Banggi Island, and 30 in primary forest and 12 in disturbed forest on Balambangan Island. On Banggi and Balambangan islands, they were most often caught in snap traps, whereas all six individuals from Malawali were caught in cage traps. At Site A2 on Banggi Island, they were most abundant on high ground above 100 m elevation. On Banggi Peak above 350 m, 20 trap-nights with Victor snap traps caught six individuals. On Balambangan Island at Site B1 between 8 and 13 March, one subadult male had testes measuring 15 × 6 mm, and four adult males had testes measuring 19 × 9, 21 × 9, 19 × 7, and 23 × 11 mm. At Site B2 between 10 and 16 May, three adult males had testes measuring 28 × 16, 24 × 10, and 18 × 12 mm, two subadult males had testes measuring 18 × 9 and 22 × 15 mm, and one female carried three embryos measuring 6, 4, and 4 mm CRL. On Banggi, one adult male taken on 29 April at Site A2 had testes measuring 26 × 13 mm. External and cranial measurements of Banggi, Balambangan, and Malawali specimens (Table 11) are similar to those of specimens from mainland Borneo (Davis, 1962; Medway, 1977; Payne et al., 1985) and identical to those of a series from the same islands collected by Chasen and Kloss (1931).

Specimens examined—Total 79. Banggi: Site A1 (5 FMNH, 5 UKMS), Site A2 (17 FMNH, 3 UKMS). Balambangan: Site B1 (32 FMNH, 10 UKMS), Site B2 (1 FMNH). Malawali: Site C1 (1 FMNH, 2 UKMS), Site C2 (2 FMNH, 1 UKMS).

Maxomys whiteheadi—Whitehead's rat is a species confined to Thailand, Peninsular Malaysia, Sumatra, Borneo, and adjacent islands, including Banggi, Balambangan, Malawali, and Miang Besar (Medway, 1977; Payne et al., 1985). Two subspecies are known in Borneo: *M. w. whiteheadi*, found throughout the area on mainland Borneo, including Mt. Kinabalu up to 2100 m, and *M. w. piratae*, found only on Banggi, Balambangan, and Malawali islands (Payne et al., 1985). External and cranial variation among island populations (*M. w. piratae*) is discussed by Corbet and Hill (1992). Previous collectors obtained seven *M. w. piratae* specimens from Banggi Island, nine from Balambangan Island, and four from Malawali Island (Chasen & Kloss, 1931; Medway, 1965, 1977). My survey indicated that this is the most abundant small, nonvolant mammal on the three islands; 146 individuals were taken on Malawali Island (out of a total of 229 individuals of all species), 51 on Balambangan Island (out of 198 total), and 60 on Banggi Island (out of 265 total) (Table 1). However, none were taken on Molleangen Island. On Malawali Island, between 24 March and 1 April at Site C1, one adult female had one embryo measuring 25 mm CRL, and two adult males had testes measuring 23 × 12 and 20 × 10 mm; between 25 and 29 May at Site C2, three adult males had testes measuring 18 × 12, 17 × 10, and 20 × 10 mm. Five adult males taken between 8 and 13 March at Site B1 on Balambangan Island had testes rang-

ing between 14 × 9 and 22 × 13 mm, and one subadult male had testes measuring 15 × 7 mm. On the same island between 10 and 16 May at Site B2, two males had testes measuring 20 × 10 and 16 × 11 mm. External and cranial measurements (Table 11) are within the range of several series from mainland Borneo (Lyon, 1911; Gyldenstolpe, 1920; Chasen & Kloss, 1931; Davis, 1962; Payne et al., 1985) and identical to those of specimens collected by Chasen and Kloss (1931) from the same islands. However, the external measurements of these specimens (Table 11) are slightly larger than those of a pair collected from Mt. Kinabalu (Thomas, 1894).

Specimens examined—Total 255. Banggi: Site A1 (13 FMNH, 11 UKMS), Site A2 (15 FMNH, 8 UKMS). Balambangan: Site B1 (19 FMNH, 14 UKMS), Site B2 (16 FMNH, 7 UKMS). Malawali: Site C1 (49 FMNH, 28 UKMS), Site C2 (59 FMNH, 16 UKMS).

Niviventer cremoriventer—The dark-tailed tree rat is a widespread species, inhabiting areas from Burma south to Java and Borneo (Musser, 1973; Payne et al., 1985). It is also found on offshore islands near Peninsular Malaysia (Penang, Langkawi, and Tioman) and Borneo (Banggi, Balambangan, and Malawali) (Medway, 1965, 1977; Musser, 1981). Chasen and Kloss (1931) caught four specimens on Banggi Island, two on Balambangan Island, and three on Malawali Island and designated them as *N. c. malawali,* distinct from the mainland race, *N. c. kina.* Medway (1965, 1977) and Payne et al. (1985) also considered these two subspecies to be distinguishable, with the island race duller in color than the mainland race. However, on the basis of external and cranial measurements, Musser (1973) concluded that specimens from mainland Sabah are indistinguishable from the island race. On mainland Borneo, this species has been reported from a variety of habitats, but I found most individuals in primary forest at my sites on Banggi, Balambangan, and Malawali islands. On Malawali Island at Site C1 between 24 March and 1 April, one subadult and one adult female each had one fetus measuring 25 and 23 mm CRL, and four adult males had testes measuring 12 × 9, 13 × 8, 14 × 8, and 14 × 8 mm. One adult male from Site B1 on Balambangan Island on 9 March and one adult male from Site A2 on Banggi Island on 28 April had testes measuring 17 × 7 and 15 × 7 mm, respectively. External and cranial measurements of Banggi, Balambangan, and Malawali specimens (Table 11) are slightly larger than those of specimens from mainland Borneo (Chasen & Kloss, 1931; Musser, 1973; Payne et al., 1985), but they are slightly smaller than those of a series from the same islands collected by Chasen and Kloss (1931). Further, external and cranial measurements of the specimens from Banggi Island are slightly larger than those of series from Balambangan and Malawali islands.

Specimens examined—Total 60. Banggi: Site A1 (6 FMNH, 6 UKMS), Site A2 (4 FMNH, 1 UKMS). Balambangan: Site B1 (5 FMNH, 3 UKMS), Site B2 (6 FMNH). Malawali: Site C1 (6 FMNH, 7 UKMS), Site C2 (11 FMNH, 5 UKMS).

Rattus tanezumi diardii—The house rat is a common and worldwide commensal species. Medway and Yong (1976) and Musser and Califia (1982) considered this rat to have been introduced to the Sunda Shelf from an unknown area outside this region. In using the name *Rattus tanezumi,* I follow Musser and Carleton (1993), who have split this species from *Rattus rattus.* I caught two specimens at Site A2 on Banggi Island in live traps baited with banana set in a coconut plantation about 100–200 m from houses. I found field identification of this species to be difficult; individuals had light brown upperparts with milky white underparts, characteristic of *R. tiomanicus jalorensis* as described by Medway (1969), Payne et al. (1985), and Musser and Califia (1982). However, external measurements (Table 11) are larger than those of *R. tiomanicus* from the same island, but they fall within the range of *R. tanezumi* from mainland Borneo (Payne et al., 1985). Cranial measurements of both male and female specimens fall within the range of those of six adult *R. tanezumi* specimens from various localities on mainland Borneo that are available in the FMNH collection, but they differ from those of *R. tiomanicus* from Borneo. Cranial measurements of these specimens are identical to those reported for *R. tanezumi diardii* (Medway, 1966; Musser & Califia, 1982).

Specimens examined—Total 2. Banggi: Site A2 (2 FMNH).

Rattus tiomanicus—The Malaysian field rat is widely distributed in the area of Peninsular Malaysia, Sumatra, Java, and Borneo, including offshore islands at the north, east, south, and west (Medway, 1977; Musser & Califia, 1982; Payne et al., 1985). Four subspecies can be distinguished, based on underpart coloration and skull measurements: *R. t. sabae,* widespread throughout Sabah, northern Sarawak, and part of East Kalimantan; *R. t. jalorensis,* recorded from Sarawak as far north as the Baram and part of east and west Kalimantan; *R. t. banguei,* known only on Banggi and Malawali islands; and *R. t. mara,* known only from

TABLE 11. Means (± SD) and ranges of selected measurements of adult Muridae. Sample sizes (N) are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Rostral length	Orbital length
Maxomys surifer							
Banggi	m	3	40.55	19.71	15.26	18.01	13.49
			(36.96–42.94)	(17.71–20.88)	(14.30–16.12)	(15.58–19.61)	(12.57–13.97)
	f	3	39.07	18.60	14.72	17.18	13.03
			(38.08–40.42)	(18.18–19.03)	(14.67–14.79)	(16.98–17.35)	(12.76–13.31)
Balambangan	m	4	41.47 ± 2.13	19.72 ± 1.16	14.96 ± 0.37	17.95 ± 1.17	13.57 ± 0.86
			(38.80–43.98)	(18.10–20.68)	(14.83–15.44)	(16.39–19.02)	(12.30–14.20)
	f	2	39.70	19.00	14.37	17.92	13.08
			(36.85–42.54)	(18.19–19.88)	(14.22–14.51)	(16.80–19.04)	(12.42–13.74)
Malawali	m	2	35.51	18.64	14.59	16.45	12.12
			(33.00–38.01)	(18.46–18.82)	(14.55–14.63)	(16.16–16.73)	(11.94–12.31)
	f	1	37.55	18.92	13.95	16.66	12.55
			—	—	—	—	—
Maxomys whiteheadi							
Banggi	m	5	30.44 ± 1.73	14.97 ± 0.38	12.51 ± 0.28	12.80 ± 1.07	10.77 ± 0.54
			(28.75–33.14)	(14.54–15.43)	(12.24–12.86)	(11.76–14.54)	(10.34–11.58)
	f	1	30.06	15.22	12.43	12.54	10.10
			—	—	—	—	—
Balambangan	m	2	30.64	15.60	12.68	12.49	10.45
			(29.20–32.07)	(14.92–16.28)	(12.33–13.03)	(11.93–13.05)	(10.37–10.52)
	f	3	30.46	15.10	12.58	13.09	10.46
			(29.88–31.08)	(14.80–15.64)	(12.36–12.70)	(12.81–13.46)	(10.16–10.90)
Malawali	m	4	31.21 ± 0.23	15.23 ± 0.25	12.45 ± 0.26	12.69 ± 0.26	10.55 ± 0.37
			(30.90–31.40)	(14.89–15.44)	(12.21–12.82)	(12.32–12.95)	(10.24–11.09)
	f	5	30.35 ± 0.62	15.31 ± 0.44	12.32 ± 0.39	12.44 ± 0.37	10.52 ± 0.33
			(29.68–31.36)	(14.79–15.97)	(11.71–12.64)	(12.09–13.08)	(10.20–10.84)
Niviventer cremoriventer							
Banggi	m	5	31.24 ± 0.59	15.49 ± 0.18	12.85 ± 0.31	12.55 ± 0.53	11.34 ± 0.23
			(30.34–31.83)	(15.33–15.69)	(12.52–13.30)	(11.81–12.80)	(11.06–11.66)
	f	2	29.36	15.10	12.80	12.01	10.85
			(28.83–29.88)	(15.04–15.15)	(12.62–12.97)	(11.91–12.10)	(10.71–10.99)
Balambangan	m	5	33.41 ± 1.30	17.01 ± 0.89	13.64 ± 0.36	13.72 ± 0.45	11.83 ± 0.45
			(31.26–34.53)	(15.58–17.92)	(13.01–13.91)	(12.92–13.96)	(11.22–12.33)
	f	4	32.53 ± 1.41	16.52 ± 0.79	13.15 ± 0.31	13.59 ± 1.02	11.71 ± 0.24
			(30.75–34.17)	(15.60–17.51)	(13.02–13.61)	(12.53–14.98)	(11.50–11.98)
Malawali	m	5	33.73 ± 0.90	16.95 ± 0.13	13.31 ± 0.26	13.44 ± 1.86	11.49 ± 0.19
			(32.28–34.40)	(16.79–17.14)	(12.96–13.61)	(13.38–14.78)	(11.24–11.72)
	f	5	32.43 ± 1.19	16.54 ± 0.40	12.95 ± 0.25	13.41 ± 0.64	11.22 ± 0.35
			(30.45–33.39)	(15.92–16.93)	(12.74–13.36)	(12.41–14.01)	(10.64–11.53)
Rattus tanezumi diardii							
Banggi	m	1	37.80	17.67	15.31	14.15	13.92
			—	—	—	—	—
	f	1	37.03	17.59	14.57	13.71	13.28
			—	—	—	—	—
Rattus tiomanicus							
Banggi	m	1	—	18.51	—	14.05	13.92
			—	—	—	—	—
Balambangan	f	—	—	—	—	—	—
			—	—	—	—	—
Malawali	m	1	39.11	19.53	16.15	14.78	14.40
			—	—	—	—	—
	f	2	42.90	20.69	16.16	16.12	15.28
			(42.60–43.19)	(20.28–21.10)	(16.01–17.19)	(15.60–16.64)	(15.20–15.35)

TABLE 11. *Extended.*

Molariform toothrow	Palatal breadth at M^3	Diastema length	N	Total length	Tail length	Forearm length	Weight (g)
6.59	7.72	12.52	17	353.5 ± 29.5	173.1 ± 14.5	39.1 ± 2.5	138.7 ± 36.6
(6.41–6.82)	(7.09–8.07)	(10.73–13.43)		(309–399)	(154–200)	(32–43)	(97–205)
6.52	7.67	12.01	5	347.2 ± 36.7	172.0 ± 15.0	39.2 ± 1.6	125.8 ± 26.1
(6.35–6.61)	(7.35–7.84)	(11.77–12.31)		(305–391)	(149–188)	(37–41)	(85–155)
6.65 ± 0.12	7.86 ± 0.25	12.54 ± 0.97	11	345.4 ± 17.0	168.1 ± 7.2	40.2 ± 1.4	165.0 ± 27.3
(6.48–6.76)	(7.64–8.10)	(11.18–13.48)		(324–374)	(160–182)	(38–43)	(130–210)
6.31	7.79	12.35	4	347.5 ± 18.5	164.8 ± 6.8	37.5 ± 3.0	143.8 ± 33.3
(6.22–6.40)	(7.50–8.08)	(11.42–13.28)		(330–372)	(158–174)	(33–39)	(115–190)
6.31	7.74	11.17	4	322.8 ± 12.9	158.8 ± 6.3	38.8 ± 1.3	120.8 ± 22.0
(6.21–6.41)	(7.72–7.75)	(10.74–11.59)		(309–339)	(154–168)	(37–40)	(100–149)
5.86	7.53	11.46	1	351.0	163.0	37.0	140.0
—	—	—		—	—	—	—
5.54 ± 0.26	5.89 ± 0.22	8.67 ± 0.49	10	230.4 ± 14.2	100.8 ± 5.8	28.1 ± 1.7	52.3 ± 9.2
(5.33–5.96)	(5.54–6.15)	(8.20–9.45)		(214–251)	(91–111)	(26–31)	(42–65)
5.74	5.97	8.19	10	227.2 ± 14.4	101.0 ± 14.2	27.6 ± 0.7	51.9 ± 8.1
—	—	—		(203–239)	(96–124)	(27–29)	(41–63)
5.42	6.27	8.86	10	241.5 ± 13.9	106.3 ± 9.2	28.2 ± 1.5	74.3 ± 9.7
(5.36–5.47)	(6.01–6.52)	(8.18–9.53)		(220–259)	(92–123)	(26–31)	(62–90)
5.54	6.07	8.40	8	239.9 ± 17.7	108.9 ± 9.0	27.4 ± 1.7	62.4 ± 8.8
(5.45–5.66)	(5.96–6.27)	(7.60–8.95)		(209–257)	(98–123)	(26–31)	(50–74)
5.76 ± 0.17	5.97 ± 0.13	8.82 ± 0.14	10	244.4 ± 12.6	107.0 ± 6.9	28.4 ± 1.4	67.7 ± 9.3
(5.53–5.92)	(5.81–6.08)	(8.68–8.95)		(227–254)	(101–118)	(27–31)	(49–80)
5.67 ± 0.22	6.02 ± 0.10	8.66 ± 0.35	10	215.3 ± 12.4	88.2 ± 30.5	26.7 ± 10.6	47.6 ± 8.4
(5.49–6.03)	(5.92–6.15)	(8.40–9.25)		(198–232)	(87–105)	(25–28)	(33–59)
6.01 ± 0.08	6.17 ± 0.12	8.84 ± 0.38	6	323 ± 9.4	184.7 ± 11.1	27.7 ± 1.0	70.2 ± 5.4
(5.90–6.10)	(5.99–6.31)	(8.30–9.24)		(312–339)	(173–201)	(26–29)	(60–75)
6.04	6.17	8.46	4	294.5 ± 10.5	166.8 ± 6.6	27.0 ± 1.4	50.5 ± 6.6
(5.99–6.08)	(6.13–6.21)	(8.43–8.48)		(283–308)	(161–175)	(26–29)	(42–75)
6.27 ± 0.20	6.66 ± 0.13	9.76 ± 0.74	4	368.0 ± 20.2	211.8 ± 8.8	29.8 ± 1.9	83.8 ± 11.6
(5.96–6.46)	(6.55–6.83)	(8.50–10.41)		(344–394)	(204–224)	(27–31)	(69–94)
6.10 ± 0.13	6.67 ± 0.20	9.37 ± 0.74	4	351.3 ± 21.2	203.3 ± 12.0	29.8 ± 1.5	73.3 ± 8.2
(5.90–6.20)	(6.48–6.91)	(8.50–10.31)		(328–373)	(191–214)	(28–31)	(63–83)
6.40 ± 0.13	6.46 ± 0.12	9.61 ± 0.47	8	348.5 ± 21.5	197.9 ± 19.8	29.8 ± 1.0	81.6 ± 15.9
(6.19–6.55)	(6.34–6.63)	(8.91–10.03)		(312–368)	(157–216)	(29–32)	(50–91)
6.27 ± 0.14	6.43 ± 0.15	9.07 ± 0.57	10	335.2 ± 27.7	193.1 ± 17.2	29.0 ± 3.1	71.8 ± 13.7
(6.13–6.50)	(6.20–6.61)	(8.39–9.77)		(303–348)	(171–229)	(26–37)	(54–95)
6.79	7.11	11.32	1	322.0	168.0	32.0	92.0
—	—	—		—	—	—	—
6.53	6.90	10.89	1	321.0	155.0	33.0	82.0
—	—	—		—	—	—	—
6.92	7.02	10.97	1	374.0	196.0	35.0	150.0
—	—	—		—	—	—	—
—	—	—	1	389.0	194.0	37.0	160.0
—	—	—		—	—	—	—
6.65	7.66	11.49	1	371.0	198.0	39.0	110.0
—	—	—		—	—	—	—
7.32	7.91	12.32	4	361.5 ± 45.2	186.3 ± 32.9	37.5 ± 2.5	142.5 ± 35.9
(7.20–7.44)	(7.69–8.13)	(11.94–12.70)		(299–391)	(140–215)	(34–40)	(110–190)

(*cont.*)

TABLE 11. *Continued.*

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Rostral length	Orbital length
Molleangen	m	5	38.94 ± 2.97 (34.99–42.24)	18.51 ± 1.12 (16.91–19.95)	15.64 ± 0.67 (14.88–16.61)	14.72 ± 1.47 (13.12–16.36)	14.09 ± 1.27 (12.30–15.47)
	f	2	37.36 (33.53–41.18)	19.06 (16.90–21.22)	15.46 (14.51–16.41)	14.38 (12.95–15.81)	13.76 (12.10–15.42)
Sundamys muelleri							
Banggi	m	4	48.65 ± 1.80 (47.09–50.44)	25.06 ± 0.65 (24.29–25.83)	19.18 ± 0.69 (18.31–19.87)	20.28 ± 1.10 (19.11–21.28)	17.84 ± 1.05 (16.84–19.31)
	f	5	48.80 ± 1.59 (46.73–49.71)	25.33 ± 0.82 (24.89–25.69)	18.93 ± 0.49 (18.17–19.11)	20.41 ± 1.02 (19.20–22.14)	17.76 ± 0.93 (17.12–18.63)
Balambangan	m	4	44.49 ± 1.48 (42.37–45.14)	23.72 ± 1.17 (22.48–25.24)	17.58 ± 0.69 (16.96–18.43)	18.05 ± 0.71 (16.99–18.48)	17.00 ± 0.50 (16.42–17.64)
	f	5	45.38 ± 2.78 (42.16–48.98)	24.02 ± 1.36 (22.55–25.57)	17.80 ± 1.00 (16.35–18.73)	17.56 ± 1.88 (14.88–18.88)	17.20 ± 1.15 (16.07–18.80)
Malawali	m	2	38.50 (37.55–39.45)	21.16 (20.83–21.48)	15.49 (15.27–15.71)	14.98 (14.10–15.86)	14.42 (14.16–14.68)
	f	5	39.38 ± 1.48 (37.32–40.98)	21.48 ± 0.85 (20.35–22.26)	15.89 ± 0.40 (15.29–16.34)	15.97 ± 0.66 (15.31–16.60)	14.98 ± 0.63 (14.13–15.58)
Molleangen	m	2	47.44 (43.74–51.13)	25.35 (24.00–26.69)	18.74 (18.09–19.39)	19.51 (17.68–21.33)	17.98 (17.03–18.93)
	f	6	47.00 ± 1.59 (43.91–48.41)	24.75 ± 0.56 (24.21–25.45)	18.50 ± 0.64 (17.60–19.12)	18.87 ± 1.01 (17.12–20.10)	17.93 ± 0.51 (17.07–18.47)

Note: Measurements other than weight are in millimeters.

Maratua Archipelago off eastern Borneo (Medway, 1977; Musser & Califia, 1982; Payne et al., 1985). Chasen and Kloss (1931) obtained five specimens from Banggi Island and one adult male on Malawali Island. These specimens were initially identified as *Rattus rattus banguei* by Chasen and Kloss (1931), but they were assigned to *Rattus tiomanicus* when that species was recognized as distinct from *Rattus rattus* (Davis, 1962; Medway, 1977). *R. tiomanicus* can be distinguished from *Rattus tanezumi* (formerly part of *R. rattus*) based on pelage, which is more sleek over the upperparts, and by relatively short incisive foramina, short maxillary toothrows, and weakly developed supraorbital ridges compared to *R. tanezumi* (Medway & Lim, 1966; Musser & Califia, 1982). Malawali specimens, taken between 24 and 28 March at Site C1, included a female with one fetus measuring 25 mm CRL and an adult male with testes measuring 13 × 10 mm, and from Site C2 between 25 and 29 May, an adult male with testes measuring 18 × 10 mm. Three adult males taken between 8 and 13 April at Site D2 on Molleangen Island had testes measuring 17 × 15, 25 × 16, and 25 × 16 mm, and one juvenile male from Site D1 had testes measuring 8 × 5 mm. External and cranial measurements of single specimens from Banggi and Balambangan islands and the means of specimens from Molleangen and Malawali (Table 11) are slightly greater than those of specimens from mainland Borneo (Medway, 1977; Musser & Califia, 1982; Payne et al., 1985).

Specimens examined—Total 57. Banggi: Site A2 (1 FMNH). Balambangan: Site B2 (1 FMNH). Malawali: Site C1 (12 FMNH, 3 UKMS), Site C2 (4 FMNH, 1 UKMS). Molleangen: Site D1 (22 FMNH, 4 UKMS), Site D2 (6 FMNH, 3 UKMS).

Sundamys muelleri—Muller's rat is one of the largest rat species in Borneo. It is distributed throughout Southeast Asia, and near Borneo it is present on many offshore islands off the west and southeast coasts, including Lamukotan and Sebuku (Medway, 1977; Musser & Newcomb, 1983; Payne et al., 1985). Chasen and Kloss (1931) collected 11 specimens on Banggi Island and five on Balambangan Island. I caught this species on Banggi, Balambangan, and Malawali islands, mostly in primary forest on low ground and near streams. On Molleangen Island, four specimens were taken between 8 and 13 April from Site D2; two adult males and one subadult male had testes measuring 23 × 22, 25 × 14, and 14 × 6 mm, respectively, and one adult female had five embryos of 43, 40, 43, 44, and 52 mm CRL. On Balambangan Island, one adult male taken on 11 March at Site B1 had testes measuring 19 × 7

TABLE 11. *Extended. Continued.*

Molariform toothrow	Palatal breadth at M^3	Diastema length	N	Total length	Tail length	Forearm length	Weight (g)
6.87 ± 0.26	7.23 ± 0.32	11.43 ± 1.08	9	352.9 ± 28.5	176.9 ± 28.2	36.8 ± 1.9	150.6 ± 21.3
(6.67–7.32)	(6.89–7.63)	(9.86–12.48)		(319–391)	(118–215)	(35–41)	(120–195)
6.95	7.28	10.41	2	357.5	199.5	35.5	172.0
(6.34–7.55)	(6.75–7.80)	(9.52–11.30)		(308–407)	(171–228)	(34–37)	(154–190)
9.64 ± 0.47	9.44 ± 0.32	14.35 ± 0.57	10	478.2 ± 21.7	270.0 ± 37.5	46.9 ± 2.1	244.0 ± 54.0
(9.09–10.18)	(9.06–9.81)	(13.73–14.85)		(456–524)	(249–275)	(45–49)	(150–300)
9.81 ± 0.55	9.45 ± 0.27	14.37 ± 0.49	10	460.0 ± 26.1	244.1 ± 18.6	46.0 ± 3.1	232.5 ± 21.3
(9.47–9.93)	(9.24–9.73)	(12.96–14.83)		(427–498)	(215–267)	(38–49)	(200–260)
9.09 ± 0.26	8.95 ± 0.22	13.02 ± 0.59	10	448.8 ± 26.8	229.5 ± 17.3	42.7 ± 1.4	219.0 ± 59.7
(8.83–9.39)	(8.75–9.25)	(12.32–13.75)		(408–498)	(205–264)	(40–45)	(120–310)
9.04 ± 0.36	9.08 ± 0.64	13.37 ± 0.96	10	430.6 ± 23.5	219.8 ± 11.2	42.1 ± 20.1	208.5 ± 36.3
(8.49–9.44)	(8.02–9.76)	(11.89–14.24)		(387–461)	(201–231)	(38–44)	(125–250)
8.56	8.28	10.97	2	345.0	175.5	39.0	113.0
(8.39–8.73)	(8.22–8.33)	(10.84–11.09)		(342–348)	(155–196)	(37–41)	(96–130)
8.37 ± 0.12	8.24 ± 0.18	11.24 ± 0.67	6	378.2 ± 34.1	207.7 ± 12.1	39.3 ± 1.9	165.8 ± 23.3
(8.18–8.51)	(8.05–8.43)	(10.06–11.68)		(318–418)	(191–228)	(37–42)	(140–190)
9.63	9.92	13.28	11	475.8 ± 21.1	249.4 ± 14.0	47.1 ± 2.2	274.1 ± 41.5
(9.51–9.74)	(9.61–10.23	(12.13–14.42)		(429–506)	(228–271)	(43–51)	(200–320)
9.11 ± 0.15	9.37 ± 0.22	13.51 ± 0.67	10	453.7 ± 15.6	239.0 ± 16.0	44.8 ± 1.6	251.5 ± 35.0
(8.88–9.33)	(9.07–9.68)	(12.37–14.11)		(436–486)	(217–269)	(43–48)	(200–335)

mm; at Site B2 between 10 and 15 May, three adult males had testes measuring 15 × 8, 14 × 9, and 14 × 8 mm, and one subadult male had testes measuring 6 × 4 mm. Three adult males taken between 26 April and 2 May at Site A2, Banggi Island, had testes measuring 15 × 7, 13 × 6, and 17 × 10 mm. External and cranial measurements of specimens from Banggi, Balambangan, and Molleangen (Table 11) fall within the range of specimens from mainland Borneo (Davis, 1962; Medway, 1977; Payne et al., 1985). However, external and cranial measurements of specimens from Malawali Island (Table 11) are smaller than those from Banggi, Balambangan, and Molleangen, and from mainland Borneo. Chasen (1935) identified Banggi and Balambangan specimens as *S. m. otiosus* on the basis of a shorter tail length than the subspecies from mainland Borneo, *S. m. borneanus*. However, Musser and Newcomb (1983) further analyzed the same specimens examined by Chasen (1935) and concluded that these two subspecies are morphologically the same.

Specimens examined—Total 146. Banggi: Site A1 (19 FMNH, 3 UKMS), Site A2 (12 FMNH, 3 UKMS). Balambangan: Site B1 (12 FMNH, 10 UKMS), Site B2 (18 FMNH, 14 UKMS). Malawali: Site C1 (6 FMNH, 6 UKMS), Site C2 (2 FMNH, 1 UKMS). Molleangen: Site D1 (9 FMNH, 11 UKMS), Site D2 (10 FMNH, 10 UKMS).

Order Carnivora
Family Mustelidae—Weasels and Otters

Lutra perspicillata—This species is distributed throughout island and mainland Southeast Asia (Payne et al., 1985). On Banggi, otter tracks were seen on a beach at Wak-wak (Site A1) on 9 February. On 23 February I observed three individuals swimming in the open sea near the southeastern part of Molleangen. Wells (1977) collected *Lutra perspicillata* on Balambangan, and it is likely that the otters on Banggi and Molleangen belong to this species. The adult collected by Wells (1977) was from a reed marsh.

No specimens were examined.

Family Viverridae—Civets

Arctogalidia trivirgata—The small-toothed palm civet is an arboreal species known from islands offshore of Peninsular Malaysia and Singapore, but it has not been reported from offshore islands near Borneo (Medway, 1969; Payne et al., 1985). One adult female was caught on Banggi Island in a locally made live trap set in a tree in disturbed forest near a small stream, at about 2 m above the ground. External measurements (Table 12) fall within the size range of specimens from mainland

TABLE 12. Means (± SD) and ranges of selected measurements of adult Viverridae. Sample sizes are given separately for cranial and external measurements.

Island	Sex	N	Condylobasal length	Zygomatic width	Mastoid width	Orbital length	C^1 to M^3	Molariform toothrow	Palatal breadth at M^3	Palatal length	N	Total length	Tail length	Forearm length	Weight (g)
Arctogalidia trivirgata															
Banggi	f	1	92.83	54.67	35.85	38.57	35.04	13.70	25.25	49.60	1	1,011.0	557.0	84.0	1,550.0
			—	—	—	—	—	—	—	—		—	—	—	—
Paradoxurus hermaphroditus															
Banggi	m	1	93.74	54.32	33.19	38.04	33.86	13.87	23.13	47.80	—	—	—	—	—
			—	—	—	—	—	—	—	—	—	—	—	—	—
Viverra tangalunga															
Banggi	m	1	105.81	51.76	35.58	35.85	41.39	17.18	19.98	50.29	—	—	—	—	—
			—	—	—	—	—	—	—	—	—	—	—	—	—

Note: Measurements other than weight are in millimeters.

Borneo; however, condylobasal length and zygomatic length are slightly smaller (Davis, 1962; Payne et al., 1985).

Specimens examined—Banggi: Site A3 (1 FMNH).

Paradoxurus hermaphroditus—The palm civet is a widespread species in Southeast Asia, reported on many islands offshore of Peninsular Malaysia, such as Tioman, Langkawi, Penang, and Singapore. The first report for the offshore islands of Borneo is an adult female I shot in selectively logged forest on 15 June at Site A3 on Banggi Island. According to local people, it is common in disturbed and primary forest throughout the island. Condylobasal length and zygomatic width (Table 12) fall within the range of a series of seven specimens from eastern Sabah (Davis, 1962).

Specimens examined—Banggi: Site A3 (1 FMNH).

Viverra tangalunga—The Malay civet (or tangalung) is a species inhabiting Peninsular Malaysia, Borneo, Sumatra, and the Philippines (Payne et al., 1985). *V. t. tangalunga* is the only subspecies known on mainland Borneo, and it has also been reported on two adjacent islands, Karimata and Laut (Medway, 1965, 1977). On Banggi Island, a single adult male was shot by a hunter in logged forest at Site A3 on 1 April. This is the most common civet on this island; I saw one individual in a logged area at Kalangkaman at about 7:30 p.m. on 29 April, and several were reported by islanders in disturbed areas adjacent to primary forest at Site A1. Only cranial measurements are available (Table 12). Condylobasal length and zygomatic width of a single specimen are smaller than those of a series of seven specimens from eastern Sabah (Davis, 1962).

Specimens examined—Banggi: Site A4 (1 FMNH).

Order Artiodactyla
Family Suidae—Pigs

Sus barbatus—The bearded pig is a common ungulate that occupies primary and secondary habitats in peninsular Malaysia, Palawan Island in the Philippines, and Borneo, including islands offshore of Sabah. On all four of these islands, I saw pig tracks near the shore and also far inland. Several were seen in a tapioca plantation at Site B1 on Balambangan Island. Because pig hunting is uncommon in this area, the pig population is high, and pigs are considered by the islanders to be a pest of cultivation.

No specimens are available.

Family Cervidae—Deer

Cervus unicolor—The sambar deer is a widespread species in Asia, including larger islands such as Penang and Singapore, off the coast of Peninsular Malaysia, and Laut, Balambangan, and Banggi, off the coast of Borneo. Chasen and Kloss (1931) obtained several pairs of antlers and skulls from Banggi Island, but not from Balambangan Island. Although deer hunting was very active on Banggi and Balambangan islands during my study, the population is large on both islands. One major factor is habitat, especially the secondary habitat that was left by several years of shifting cultivation, providing a large volume of tender young twigs and grasses. A second factor may be the absence of competition for food with other browsing ungulates, and a third may be the absence of large carnivores. Hunting was concentrated at Sites

TABLE 13. Means (± SD) and ranges of selected measurements of adult Tragulidae. Sample sizes are given separately for cranial and external measurements.

Island	Sex	N	Condylo-basal length	Zygo-matic width	Mastoid width	Rostral length	Orbital length	Molari-form toothrow	Palatal breadth at M^3
Tragulus napu									
Banggi	m	1	95.71	47.34	28.68	48.38	—	19.15	16.67
			—	—	—	—	—	—	—
Balambangan	f	1	87.10	43.33	20.14	42.34	31.47	17.23	15.41
			—	—	—	—	—	—	—

Note: Measurements other than weight are in millimeters.

A2 and A3 on Banggi Island and at Sites B1, B2, and B3 on Balambangan Island during my study.

No specimens were examined.

Family Tragulidae—Mouse Deer

Tragulus napu—The greater mouse deer is a tiny ungulate species widespread in Southeast Asia, including small islands. Chasen and Kloss (1931) collected one adult male, one adult female, and one immature female from Banggi Island on 2 September 1926 and described them as *T. n. banguei*. I saw one individual during a night survey at Site A2 in disturbed forest on Banggi Island. Two individuals were shot by hunters; one adult male was taken in selectively logged forest near Site B1 on Balambangan Island and one subadult female in mixed grass and low tree vegetation near Site A3 on Banggi Island. Only skulls were given to me; cranial measurements (Table 13) of an adult male from Banggi Island are slightly smaller than those of an adult male collected by Chasen and Kloss (1931) from the same island, and far smaller than a series from mainland Borneo (Chasen & Kloss, 1931; Davis, 1962).

Specimens examined—Total 2. Banggi: Site A1 (1 FMNH). Balambangan: Site B1 (1 FMNH).

Results and Discussion

Inventory of Mammals

As far as can be determined, mammals on Banggi, Balambangan, and Malawali islands were first collected by a party from the Raffles Museum of Singapore (Chasen & Kloss, 1931). They spent 9 days (31 August to 8 September 1927) on Banggi Island, 2 days (8 and 9 September 1927) on Malawali Island, and 5 days (9 to 14 September 1927) on Balambangan Island. Later, Wells (1977) spent only 1 day at Tanjung Periok on Balambangan Island, followed by Payne et al. (1985) on Balambangan, Banggi, and Malawali islands.

Based on published reports, I am unable to ascertain prior trapping effort and trapping methods. I believe that during the first visit by the Raffles Museum party, bats were sampled by shooting or caught by hand at roost sites, since mist nets were not available at that time. Thus, only a few bat species were reported from this visit, with many common species missed, including the abundant *Cynopterus brachyotis* and *Rousettus amplexicaudatus*. No serious attempt was made by Wells (1977) to investigate the bat fauna on Balambangan Island, from which he documented only two species, *Cynopterus brachyotis* and *Kerivoula hardwickii*. Payne et al. (1985) may have spent some time netting bats and possibly trapping bats with a harp trap on Banggi and Balambangan islands, from which they documented at least eight species of bats, but sites and times spent on these islands are not available to me.

Among nonvolant mammals, previous collectors have recorded 16 species of small and large mammals on Banggi Island (one primate, one dermopteran, three tree shrews, nine murid rodents, two ungulates), 11 species on Balambangan Island (one primate, one tree shrew, six murid rodents, three ungulates), and seven species on Malawali Island (one primate and six murid rodents). My recent survey increased by nine species the number known on Banggi Island (two primates, one murid rodent, four civets, one ungulate, and one pholidotan, excluding a commensal species of rat, *Rattus tanezumi*); by four species the number known on Balambangan Island (one insectivore, one dermopteran, and two murid rodents); and by one species of ungulate the number known on Malawali Island. The fauna of Molleangen Island, unknown prior to this study, includes four species

(two murid rodents, one ungulate, and one primate).

Among bats, a few species were recorded by earlier collectors: only four on Banggi Island and eight on Balambangan Island, with none from Malawali or Molleangen Island. Mist netting and trapping with a harp trap produced nine new records of bats on Banggi Island, 11 new species on Balambangan Island, and six species each on Malawali and Molleangen islands. Collectively, only five species of fruit bats are now known on these four islands, compared to 16 species of insectivorous bats (one megadermatid, one nycterid, five rhinolophids, and nine vespertilionids).

All 52 species of mammals known from these four islands are species mainly or exclusively found in the lowland and low hill areas on mainland Borneo. Out of a total of 25 bat species, 18 are known on Borneo only in the lowland areas below 900 m elevation, and the remaining seven are in both the lowlands and in hill areas up to 1800 m elevation (Payne et al., 1985). All nonvolant mammal species known from these four islands have been reported on the mainland in both the lowland and hill areas below 2000 m elevation, except the two species of large ungulates (*Sus barbatus* and *Cervus unicolor*) and one carnivore (*Paradoxourus hermaphroditus*), which are restricted to lowland areas, and *Crocidura fuliginosa*, which ranges from sea level up to 3700 m elevation on Mt. Kinabalu (Payne et al., 1985).

Trapping, Netting, and Visual Surveys

SMALL MAMMALS—Murid rodents were the most diverse group, representing about 24% of the species in eight mammalian families on Banggi Island, 38% of the species in six families on Balambangan Island, 62% of the species in four families on Malawali Island, and 50% of the species in three families on Molleangen Island (Table 14).

Sundamys muelleri and *Rattus tiomanicus* were two murid species found on all four islands; the former was most common on Molleangen and Balambangan and the latter species on Molleangen and Malawali. Three additional species, *Maxomys whiteheadi*, *Niviventer cremoriventer*, and *Maxomys surifer*, were found on the three largest islands; the first two were common and abundant on Malawali and Banggi islands. The last species was found at high density on Banggi and Balambangan islands, but it was rare on Malawali Island.

The order Scandentia is represented by three species, *Tupaia gracilis*, *Tupaia minor*, and *Tupaia tana*. All occur on Banggi Island, and one species, *Tupaia minor*, was found on Balambangan Island. The latter two species were very common in primary and secondary forest, but the first species was confined to primary forest on the largest island.

Of the six sciurids known from the four islands, all were found on Banggi Island, except one (*Callosciurus notatus*), which was found only on Malawali Island. Only three species of this family were on Balambangan Island: *Callosciurus prevostii*, *Sundasciurus lowii*, and *Exilisciurus exilis*. Some species of this family, *Callosciurus notatus* and *Callosciurus prevostii*, were strikingly abundant in disturbed forest and in plantations, where they feed largely on crop plants such as coconuts. *Petaurista petaurista* was often seen in selectively logged forest, and was seen to feed on figs on Banggi Island. *Ratufa affinis* was very common in tall primary forest on Banggi Island, but it was very difficult to sample. *Sundasciurus lowii* was moderately common and was frequently caught and seen in secondary forest on both Banggi and Balambangan islands.

From the field trapping, I recorded 265 captures in 965 trap-nights on Banggi Island, 198 captures in 1,058 trap-nights on Balambangan Island, 229 captures in 940 trap-nights on Malawali Island, and 77 captures in 954 trap-nights on Molleangen Island (Table 1). The cumulative number of species captured reached an asymptote at 60 trap-nights on Molleangen Island and 142 traps-nights on Malawali Island (Fig. 10). On Banggi and Balambangan islands there was no increase in the total number of species after 798 and 875 trap-nights, respectively (Fig. 10). Based on the cumulative number of species caught after about 1,000 trap-nights, I am convinced that my trapping effort on these islands was at least minimally adequate. It is parallel to the studies in the Philippines that indicate that 900 trap-nights are adequate to document species richness (Heaney et al., 1989; Rickart et al., 1991). However, rare species such as *Crocidura fuliginosa* and *Exilisciurus exilis* can still be missed, especially on large islands. *Crocidura fuliginosa* was trapped only on Balambangan, but *Exilisciurus exilis* was not collected from any islands, although it was previously reported on Banggi Island.

The percent of successful capture on all four islands varied from 8.4/100 trap-nights in primary forest on Molleangen Island to 31.6/100 trap-nights in secondary forest on Banggi Island. Trapping

success in both primary and secondary habitats was highest on Banggi and Malawali islands: 24.6 and 25.6 in primary forest and 31.6 and 27.8 in disturbed forest, respectively. Trap success was moderately low on Balambangan Island (17.7 and 22.9 in primary and disturbed habitats) and lowest on Molleangen Island (8.4 and 15.4 in primary and disturbed habitat) (Table 1). These results also show that the percent of successful capture on each island was higher in disturbed forest than in primary forest; on Banggi, Balambangan, and Malawali islands, success was slightly higher in secondary forest but was double on Molleangen Island. The same pattern was reported on Tioman Island near Peninsular Malaysia by Medway (1966) and on Catanduanes Island in the Philippines (Heaney et al., 1991). Although the percent of successful capture was higher in disturbed forest, the species richness was higher in primary forest on two of the islands, Banggi and Malawali, and at the same number of species on Banggi and Molleangen (Table 1).

Medway (1966) made a rough comparison between trap success in primary forest on the mainland near Kuala Lumpur, Peninsular Malaysia and that in primary forest on Tioman Island, and he found Tioman Island to exhibit trap success five times higher than the mainland (5.0 and 28.6 per 100 trap-nights, respectively; Medway, 1966). Although no comparable data are available from the mainland of Sabah, results show the same pattern; trap success in this study was two to five times higher than trap success in primary forest near Kuala Lumpur reported by Medway (1966), two to eight times higher than in primary habitat between 150 m and 1000 m on Kedah Peak (3.4–6.6 per 100 trap-nights; Langham, 1975), and more than seven times higher than in mixed habitats at Pasoh, Peninsular Malaysia (1.2 per 100 trap-nights; Table 2; Kemper & Bell, 1985).

Further, there is variation in percent of trapping success in primary forest on these islands compared to several other islands in the Philippines and Peninsular Malaysia; it is 4 to 12 times higher than on Leyte Island (1.8 to 4.4 per trap-nights; Heaney et al., 1989), 2 to 5 times higher than on Negros Island (4.5 to 13.7 per 100 trap-nights; Heaney et al., 1989), and 2 times higher than on Catanduanes Island (5.2 per 100 trap-nights; Heaney et al., 1991). However, trapping success in all habitats on Banggi (25.9 per 100 trap-nights), Balambangan (19.00 per 100 trap-nights), Malawali (26.7 per 100 trap-nights), and Molleangen (9.7 per 100 trap-nights) was slightly lower than on Tioman Island (36.2 per 100 trap-nights; Medway, 1966), near Peninsular Malaysia.

There are two additional species of small mammals that were very difficult to sample or observe, and apparently low in density and very limited in distribution: *Tarsius bancanus* and *Manis javanicus*. Both species were seen only in old logged forest in the northeastern portion of Banggi Island.

Three species of civets (*Arctogalidia trivirgata, Paradoxurus hermaphroditus,* and *Viverra tangalunga*), one species of primate (*Nycticebus coucang*), and one species of dermopteran (*Cynocephalus variegatus*), although difficult to trap, were fairly common and well distributed in primary and disturbed forest on the largest island. Civets and *N. coucang* were found only on Banggi Island, but the dermopteran was found on Banggi and Balambangan islands.

LARGE MAMMALS—No large mammal trapping was done, and all specimens were obtained by shooting. Because there are not many large mammals on these islands, I have strong confidence that I have documented all large mammals. There are only three ungulate species, common and abundant in both primary and secondary forest on these islands: *Cervus unicolor, Tragulus napu,* and *Sus barbatus*. The first two species were found only on Banggi and Balambangan islands, but the latter occurs on all four islands.

FRUIT BATS—From this survey, five species of fruit bats were recorded on Banggi Island, four on Molleangen Island, and three each on Malawali and Balambangan islands (Table 15). The number of fruit bats sampled from primary forest and disturbed forest was near the minimum acceptable sampling size, and it may be subject to sampling artifacts. Netting samples of about 100 individual fruit bats from each island were suggested to be likely to approximate both species richness and proportional abundance (Heideman & Heaney, 1989).

Small pteropodids recorded in this survey include *Cynopterus brachyotis* and *Rousettus amplexicaudatus,* which were very common in primary and secondary forest on all four islands, *Eonycteris spelaea,* which was found on Banggi and Molleangen, and *Macroglossus minimus,* found on all islands except Balambangan. There is only one large pteropodid bat, *Pteropus vampyrus,* that was not sampled, but I or others have sighted it on Banggi and Balambangan islands.

I netted 226 individuals of four species on Banggi Island (94 at Site A1 and 132 at Site A2), 86 individuals of three species on Balambangan Is-

TABLE 14. List of mammal species found on Banggi, Balambangan, Malawali, and Molleangen islands.

Taxon	Banggi	Balambangan	Malawali	Molleangen
Order Insectivora—Insectivores				
Family Soricidae—Shrews				
Crocidura fuliginosa	–	+	–	–
Order Scandentia—Tree shrews				
Family Tupaiidae—Tree shrews				
Tupaia minor	+*	+*	–	–
Tupaia gracilis	+*	–	–	–
Tupaia tana	+*	–	–	–
Order Dermoptera—Colugo				
Family Cynocephalidae—Colugo				
Cynocephalus variegatus	*	+	–	–
Order Chiroptera—Bats				
Family Pteropodidae—Fruit Bats				
Cynopterus brachyotis	+	+	+	+
Eonycteris spelaea	+	–	–	+
Macroglossus minimus	+	–	+	+
Pteropus vampyrus	*	s	–	–
Rousettus amplexicaudatus	+	+	+	+
Family Megadermatidae—False Vampires				
Megaderma spasma	–	+	+	–
Family Nycteridae—Hollow-faced Bats				
Nycteris javanica	–	–	–	+
Family Rhinolophidae—Horseshoe Bats				
Hipposideros cervinus	+	+	–	–
Hipposideros diadema	+	+	–	–
Hipposideros dyacorum	–	+	–	–
Rhinolophus acuminatus	+	–	–	–
Rhinolophus borneensis	*	–	–	–
Rhinolophus trifoliatus	–	–	+	–
Family Vespertilionidae—Common Bats				
Kerivoula hardwicki	+	+	–	–
Kerivoula minuta	*	–	–	–
Miniopterus australis	+	+	–	–
Miniopterus magnater	–	*	–	–
Miniopterus schreibersii	+	–	–	–
Murina cyclotis	–	+	–	–
Murina suilla	+	–	–	–
Myotis macrotarsus	–	+*	–	–
Phoniscus atrox	–	+	–	–
Pipistrellus javanicus	–	–	+	–
Pipistrellus stenopterus	–	+	–	–
Pipistrellus vordermanni	+	–	–	–
Family Molossidae—Free-tailed Bats				
Cheiromeles torquatus	*	–	–	–
Order Primates—Prosimians, Monkeys, Apes				
Family Lorisidae—Loris				
Nycticebus coucang	+	–	–	–
Family Tarsiidae—Tarsiers				
Tarsius bancanus	+	–	–	–
Family Cercopithecidae—Monkeys				
Macaca fascicularis	+	*s	s	s

(*cont.*)

TABLE 14. *Continued.*

Taxon	Banggi	Balambangan	Malawali	Molleangen
Order Pholidota—Pangolins				
Family Manidae—Pangolins				
Manis javanica	s	–	–	–
Order Rodentia—Squirrels, Rats, and Mice				
Family Sciuridae—Squirrels				
Callosciurus prevostii	+*	+*	–	–
Callosciurus notatus	–	–	+*	–
Exilisciurus exilis	*	–	–	–
Petaurista petaurista	+	–	–	–
Ratufa affinis	+*	–	–	–
Sundasciurus lowii	+*	+	–	–
Family Muridae—Rats and Mice				
Maxomys surifer	+*	+*	+*	–
Maxomys whiteheadi	+*	+*	+*	–
Niviventer cremoriventer	+*	+*	+*	–
Rattus tanezumi diardii	+	–	–	–
Rattus tiomanicus	+*	+	+*	+
Sundamys muelleri	+*	+*	+*	+*
Order Carnivora				
Family Mustelidae—Weasels and Otters				
Lutra perspicillata	+	+*	–	+
Family Viverridae—Civets				
Viverra tangalunga	+	–	–	–
Paradoxurus hermaphroditus	+	–	–	–
Arctogalidia trivirgata	+	–	–	–
Order Arctiodactyla—Ungulate				
Family Suidae—Pigs				
Sus barbatus	s	s*	s	s
Family Cervidae—Deer and Mouse deer				
Cervus unicolor	s*	s*	–	–
Tragulus napu	+*	+*	–	–

+ Documented during this survey.
* Reported previously.
s Sighted.
– Not found.

land (62 at Site B1 and 24 at Site B2), 205 individuals of three species on Malawali Island (154 at Site C1 and 50 at Site C2), and 155 individuals of four species on Molleangen Island (112 at Site D1 and 43 at Site D2). I caught no fruit bats in the harp trap. The total number of fruit bat species on these islands is similar to the total number of fruit bats known on Singapore Island (five species; Yang et al., 1990) and Tioman Island (three species; Medway, 1966, 1969), but it is much smaller than on small islands in the Philippines (Heaney, 1991a).

The total netting success in primary and disturbed habitats was highest on Malawali and Banggi islands, with 5.30 and 4.62 bats per net-night, but it was lower on Molleangen and Balambangan islands, with 3.93 and 2.13 bats per net-night. Netting success in primary forest was lower than in disturbed forest, and it was highest in plantations. Two areas of primary forest with minimal disturbance, Site B2 on Balambangan Island and Site D2 on Malawali Island, had netting success of 1.44 (18 net-nights) and 1.73 (30 net-nights) bats per net-night, respectively, compared to a disturbed forest on Balambangan Island, with 3.17 bats per net-night, and an old coconut plantation adjacent to disturbed forest at Site D1 on Malawali Island, with the high netting success of 22.67 bats per net-night (10 net-nights) (Table 2).

My finding of higher netting success in planta-

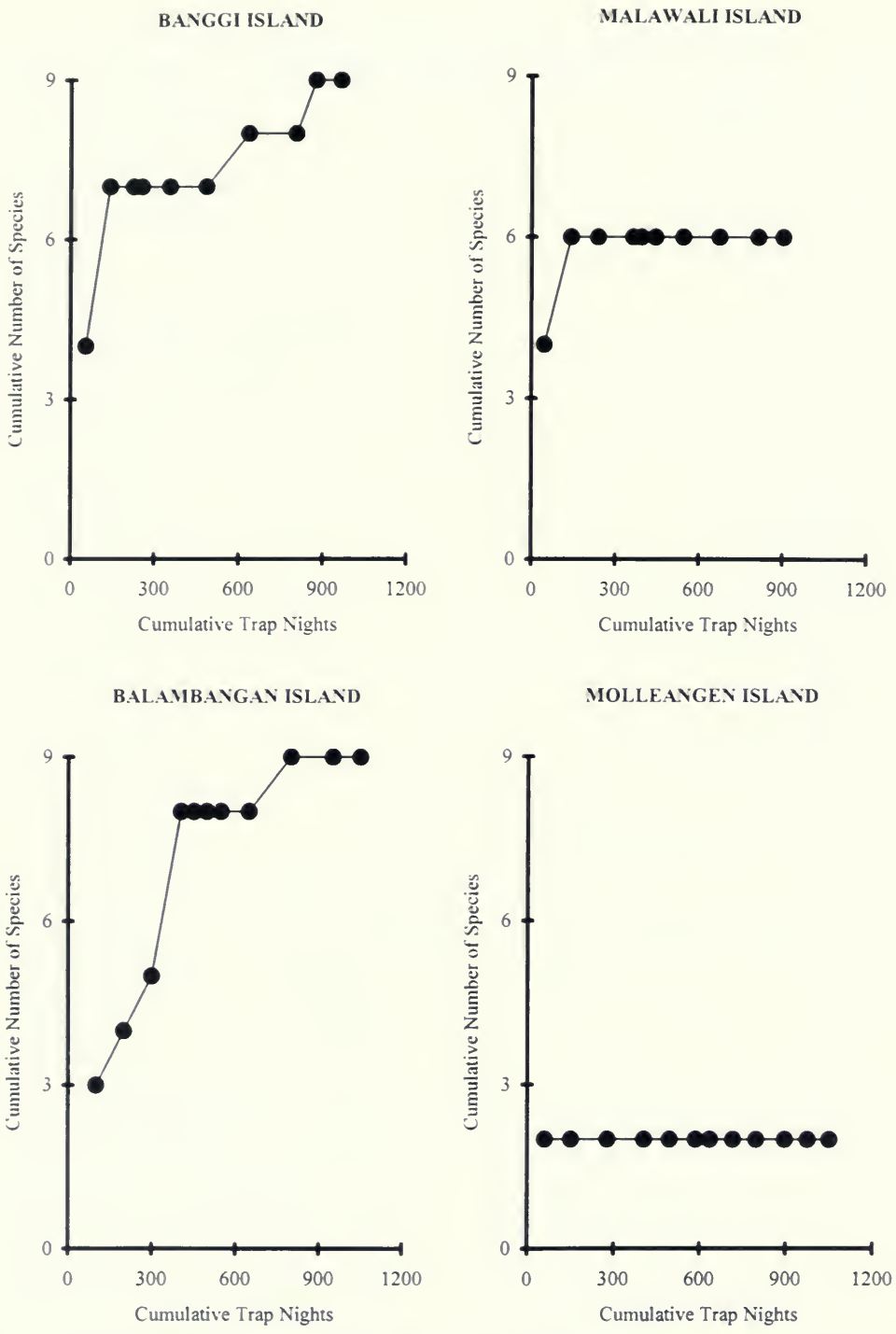

FIG. 10. Cumulative numbers of species and trap-nights on Banggi, Balambangan, Malawali, and Molleangen islands.

TABLE 15. Physical characteristics and total number of mammals found on Banggi, Balambangan, Malawali, and Molleangen islands, North Borneo.

Parameter measured	Banggi	Balambangan	Malawali	Molleangen
Area (km^2)	450	113	38	1.5
Elevation (m)	572	134	160	120
Distance from mainland (km)	12	21	9	11
Depth to large island (m)	35	35	18	14
Nonvolant species	24	14	8	4
Fruit bat species	5*	3*	3	4
Non-fruit bat species	9	10	3	2

* Plus prior record of *P. vampyrus*.

tions than in primary forest is parallel to findings on Negros and Leyte islands (10.9 to 3.9 per net-night in plantation vs. 4.4 to 0.45 per net-night in primary forest; Heaney et al., 1989). Although my forest sites on Banggi and Balambangan islands were within the range of Negros, Leyte, and Catanduanes islands (1.08 per net-night; Heaney, 1991a), my plantation site on Malawali Island had higher net success than agricultural areas on Negros and Leyte islands in the Philippines. As suggested by Heaney et al. (1989), it may be that higher netting success in plantation/agricultural areas is due to the abundance of fruit sources.

INSECTIVOROUS BATS—Because many insectivorous bats are generally difficult to catch with mist nets and not easily sampled with a harp trap (see Tuttle, 1974; Francis, 1989), I thus consider my data to be incomplete. I sampled only nine species on Banggi Island, ten on Balambangan Island, three on Malawali Island, and two on Molleangen Island.

Relatively few insectivorous bats were caught in mist nets; two individuals of two species were netted in 44 net-nights on Molleangen Island, five individuals of two species in 44 net-nights on Malawali Island, 33 individuals of six species in 45 net-nights on Balambangan Island, and 13 individuals of five species in 47 net-nights on Banggi Island. Only insectivorous bats were caught in a harp trap. In six to eight trap-nights on each island, I caught one individual of one species on Malawali Island, five individuals of two species on Banggi Island, 231 individuals of seven species on Balambangan Island, and none on Molleangen Island.

Among these four islands, based on both trapping (harp trap) and netting, Balambangan Island had the highest number of insectivorous bat species, with ten species, but the lowest number of fruit bats, with three species (Table 15). The species taken in largest numbers in the harp trap was *Miniopterus australis,* in primary forest at Site B2 on Balambangan Island. This species was also taken in mist nets at Site A2 on Banggi Island. Another common species on Balambangan Island was *Hipposideros cervinus,* which was also taken on Banggi Island.

There were six insectivorous bat species that I found only on Balambangan Island; among these, *Myotis macrotarsus* was the most common species in primary forest, and *Pipistrellus stenopterus* was the most abundant species caught in mist nets set in disturbed forest at Site A1 on Balambangan Island. The other four insectivorous bat species were uncommonly captured.

There are six bat species represented each by one individual. *Nycteris javanica* and *Murina suilla* were taken only on Molleangen Island, *Rhinolophus trifoliatus* and *Pipistrellus javanicus* were taken only on Malawali Island, and *Pipistrellus vordermanni* and *Murina cyclotis* were taken only on Banggi and Balambangan islands, respectively.

Island Biogeography

GEOLOGICAL HISTORY—The growth and recession of continental glaciers during the Pleistocene caused global changes of sea level and temperature (Heaney, 1986). Sea level was 80 m or more lower than present levels at least four times during the Pleistocene (Ollier, 1975; Verstappen, 1975; Fairbanks, 1989). This fluctuation in sea level is associated with climatic cycles and variation in the orbit of the earth around the sun (Pielou, 1991; Muller & MacDonald, 1995).

The greatest drop in sea level apparently occurred during the middle Pleistocene, about 160,000 years ago, when sea level reached 160 m below present levels (Gascoyne et al., 1970; Heaney, 1986). The Sunda Shelf islands were connected to each other and to the mainland. This

resulted in a land-bridge connection between the Palawan chain, which includes Balabac, Culion, Palawan, and Busuanga islands, and northern Borneo, because they are now separated by a channel 145 m deep. However, there was no continuous land bridge to the main body of Philippines due to several channels over 200 m deep (Dunn & Dunn, 1977; Heaney, 1984, 1985, 1986, 1991b). Lack of topographical barriers between the Sunda Shelf and the Palawan chain allowed free migration of various types of forest-dwelling species, including mammals; a large number of Asian mainland species invaded the western part of the Sunda Shelf and spread eastward as far as Borneo and the Palawan islands (Dunn & Dunn, 1977; Groves, 1985; Heaney, 1985, 1986).

During the period 35,000–25,000 BP, major recession of continental glaciers resulted in flooding of the Sunda Shelf, and the sea level increased until it reached approximately the present level. During the last glaciation, between about 25,000 and 22,000 BP, the sea level dropped to about −120 m and remained there for about 4,000 years (Dunn & Dunn, 1977; Fairbanks, 1989). At this time no land-bridge connection existed between the Palawan chain and the Sunda Shelf, which were separated by a channel, the Balabac Strait, between Banggi Island (close to Kudat Peninsula) and Balabac Island (close to the southern tip of Palawan Island) (Fig. 1). The distance between the two sides of the strait is estimated to have been about 10–12 km (Dunn & Dunn, 1977; Heaney, 1986). Because of this isolation, the Palawan chain seen today was a single large island during the late Pleistocene, but it has been isolated from its faunal source, Borneo, since the middle Pleistocene (Heaney, 1985, 1986).

Balambangan, Banggi, Malawali, and Molleangen islands lie at the eastern edge of the continental shelf north of Borneo. These islands are separated from mainland Borneo by several narrow channels 10–35 m in depth. Based on the present depth of the sea (U.S. Defense Mapping Agency; scale 1:200,000) (see Geology and Climate section, above), I estimate that these four islands (Fig. 2) were separated from mainland Borneo about 9,000 years ago. This estimation is based on data from Dunn and Dunn (1977) and Fairbanks (1989), who hypothesized that a rapid rise in sea level occurred beginning about 18,000 BP, from −120 m to a level within 10–15 m of present sea level by 6,000 BP. The current sea level was established at about 2,000 BP (Fairbanks, 1989, Fig. 2).

Patterns of Distribution—The patterns of (nonvolant) mammalian distribution on these four islands and the adjacent islands on the Sunda Shelf and the Philippines can be studied by examining the present depth of the sea separating the islands and the previous history of increasing and decreasing sea level during the Pleistocene (Heaney, 1984, 1985, 1986, 1991b; Groves, 1985). On the Sunda Shelf, species of mammals are widely distributed from island to island, especially across Peninsular Malaysia, Sumatra, and Borneo, demonstrating dispersal of mammals across the shelf during the late Pleistocene. Because these four islands are part of the Sunda Shelf and have been separated only recently from mainland Borneo, it is not surprising that all of the nonvolant mammals recorded here are purely associated with Borneo (Table 14).

Most endemic species on the Sunda Shelf are restricted to montane habitats (Heaney, 1985, 1986). Because the highest peak on Banggi Island is only 572 m, well below the lower limit of montane forest at 900 m on Borneo (Davis & Payne, 1982; Kitayama, 1992), it is again not surprising that no endemic species are present on these four islands, and that the fauna is composed entirely of lowland species found on Borneo. Borneo, the largest and highest island on the Sunda Shelf (with its peak at 4101 m on Mt. Kinabalu), has the highest percentage of endemic species, 21%, compared to Sumatra with 5%, and Java with 12% (Heaney, 1986; Earl of Cranbrook, 1988).

No endemic species were previously known on islands of the Sunda Shelf smaller than Java, a pattern supported by this study; evidence indicates that the faunas on smaller islands are relicts of the faunas on the nearest large islands (Medway, 1966; Heaney, 1984, 1986). These islands probably shared the same fauna with modern Borneo when both were part of mainland Asia, but later declined in species richness due to the extinction process that took place after isolation from mainland Borneo about 8,000–10,000 years ago (Heaney, 1986).

Extinction rates are typically high on smaller islands and lower on larger islands; thus faunas on a smaller island will be less rich than on the larger one (MacArthur & Wilson, 1963, 1967; Heaney, 1984, 1985, 1986). On these four islands, the number of nonvolant mammal species increases with island size; Molleangen Island, the smallest island in this group, has only 4 species of nonvolant mammals, composed to Malawali, the second smallest island, with 8, Balambangan, the second largest island, with 14, and Banggi, the largest island, with 24 species. Further, nonvolant mammal

species found on these islands also show the pattern of nested subsets: the fauna on a given island is a successive subset of the fauna from the next larger island (Patterson & Atmar, 1986; Patterson, 1990; Patterson & Brown, 1991). These aspects of this study will be described in more detail elsewhere (Md. Nor & Heaney, in prep.).

The nearest large islands to the north of Banggi, Balambangan, Malawali, and Molleangen islands are the islands in the Palawan chain. Despite the history of land-bridge connections during the middle Pleistocene, about 160,000 years ago, the mammals of the Palawan chain are less similar to those of these islands than are those of Borneo. Only eight species of nonvolant mammals on the islands I studied (*Tragulus napu, Manis javanicus, Rattus tiomanicus, Sundamys muelleri, Macaca fascicularis, Paradoxurus hermaphroditus, Viverra tangalunga,* and *Sus barbatus*) are represented on the islands of the Palawan chain, other than introduced commensal species (Heaney, 1986, Table 1; see also Table 14, this paper). However, endemism is high; Palawan Island has the largest number of endemic mammal species of any of the islands that were connected to the mainland during the middle Pleistocene (Groves, 1985). Nearly two-thirds of the mammals found on Palawan occur nowhere else (Groves, 1985; Heaney, 1986). Clearly, the character of the fauna of these four islands was determined overwhelmingly by the establishment of a land bridge to Borneo ca. 15,000 years ago, with scarcely a trace of the earlier connection to the islands to the north.

Conclusion

In the future, the large range of habitats on the two largest islands, Banggi and Balambangan, should be further investigated to ensure adequate mammal sampling. This includes all habitats that were not surveyed owing to time and logistical constraints during my study, especially primary habitat above 350 m on Banggi Peak, and selectively logged forest and primary lowland forest in the central portions of Banggi and Balambangan islands.

Although morphological variation in these island populations has been investigated by several researchers in the past, more thorough and complete analysis is needed, especially on the newly reported species such as insectivorous bats, civets, and primates.

The results presented above lead to several conclusions and suggestions associated with the systematics, general ecology, and evolution of mammals on these islands.

First, the number of mammal species found on these four islands was much less than in any comparable habitat on the mainland of Borneo. For example, the total number of nonvolant mammal species found on Malawali Island (Tables 4 and 5; eight species in 38 km^2) was far less than that in similar habitat, the lowland forest of Sepilok Forest Reserve (Payne, 1989; 53 species in 44 km^2). The total number of species found on Malawali Island represented only about 18% of the species found in lowland forest on mainland Borneo. Nevertheless, each small mammal fauna showed considerable diversity, especially with the new records of primates and civets on Banggi Island (Table 4). However, the large mammal taxa are generally depauperate, with only three medium- and large-size ungulates and no large carnivores.

Second, the diversity and composition of the nonvolant mammal fauna on these four islands are directly related to island size. The species on smaller islands are a subset of the next larger fauna, which is in turn a subset of the next larger fauna. These patterns support the conclusion that these are land-bridge islands that were connected both to each other and to mainland Borneo during the late Pleistocene. The rise of sea level that began about 18,000 years ago isolated these four islands from the mainland. Selective extinction appears to have predominated subsequently, and it has shaped the faunas on these islands, with species richness on each island determined by island size.

Third, the mammalian fauna on these islands is composed entirely of species found in lowland forest on Borneo. Among the four islands, Banggi is the largest and has the highest elevation, at 572 m (Banggi Peak), but it is below 900 m, the lower limit of montane forest in Borneo (Davis & Payne, 1982).

Fourth, although no endemic species are present on these islands, there are two Bornean endemic species found on Banggi Island: *Tupaia gracilis* and *Exilisciurus exilis.* This is less than 7% of the total 29 endemic species known from Borneo (Medway, 1965, 1977; Payne et al., 1985). The absence of montane and higher elevation habitats probably was the main factor restricting the presence of endemic species, because most of the endemic species on Borneo are montane species (Payne et al., 1985; Heaney, 1986). This result also supports the observation of Heaney (1986) that

no endemic species occur on Sunda Shelf islands smaller than Java (125,628 km^2).

Fifth, there was only one commensal species associated with plantations and human settlements: two individuals of *Rattus tanezumi* were sampled at Site A2 on Banggi Island, but no other commensal species such as *Rattus exulans* was found. An increase in commensal species is normally associated with destruction of natural habitats through logging and clearing for agriculture and human settlements. In the early 1920s, Merrill (1926) estimated that about 58% of Banggi Island was covered by primary forest. Although logging activity was started as early as the 1960s, I found that areas of primary forest covered about 25% of Balambangan and 30% of Banggi Island, including forest that has been selectively logged. Increased human population may soon reduce the size of natural forest; however, thus far the population on these islands has not exceeded 5,000 people at any time. Presently there are fewer than 5,000 on Banggi Island, fewer than 500 on Balambangan Island, fewer than 300 on Malawali, and fewer than 100 on Molleangen Island.

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A Selected Listing of Other Publications Having Close Ties

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